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WHITE SPOTTING IN THE FOX[1]

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THE foxes most generally raised in confinement for their furs are various color phases of the common red fox, which ranges over the northern parts of three continents —Europe, Asia and North America. It varies considerably throughout this range and systematists have at times divided the wild form into numerous species—Merriam proposed some ten or more in North America alone—but the intergradation and the apparent absence of any barrier to free interbreeding when opportunity offers would seem to make it more logical to consider the red fox a single holarctic species, *Vulpes vulpes* L. As is to be expected, mutants of the wild red are found from time to time in various localities. Aberrant pelts have long been known in the fur trade, and certain of these color variants, particularly the "blacks," have formed the basis of the fox raising industry which has assumed such considerable proportions in the past few years.

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The red fox may be superficially described as in general of a rich fulvous color with black ears, legs and feet, and with under parts and tip of tail white. More careful examination, however, reveals that the white of the under parts is not a clear white nor is it uniform throughout. It starts at the nose, runs along the sides of the jaws and

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as a band of varying width along the throat, breast and belly to the base of the tail, being narrowest at the mid-belly and wider on the throat and upper breast, and in lower belly and groin region. There may also be in some specimens some whitish on the back of the legs and even on the toes. The white areas as described are not sharply marked off from the red, but the margins tend to be indefinite, the red and white guard hairs intermingling. Furthermore, except as noted in a moment, the white is not clear, but for the most part has a dusky or "smoky" appearance due to dark underfur underlying the white guard hair. This same dusky underhair pervades all other parts of the body as well, except for the white tail-tip and occasionally small areas of variable size within the ventral white already mentioned. These smaller, pure white areas presumably correspond to the white spotting so commonly limited to the ventral side of many mammals when small in amount, but correlated with the generalized white-spotting pattern, as first clearly pointed out by Allen (1914). The more extensive dusky white on the ventral side of the red fox may be referred to as *albescence* when it is desired to distinguish it from the true white spotting. That there is a genetic difference between the two is clearly demonstrated when the one or more genes for the wild-type red drop out to give the ordinary "black" or "silver black" color phase, which is the standard ranch-raised fox of the industry. In the silver fox the red of the guard hairs and the albescent of the "white" areas is replaced by black. The silvering, which is caused by a light band on the guard hair in the red fox, remains in the black phase, giving the "standard silver." This silvering varies in amount in the wild red, and in silver foxes has been selected to produce the "quarter," "half," "three-quarter," "full silver" and paler grades of the trade. Only the pure white areas remain unchanged, irrespective of the color phase, and it is only this type of white spotting with which we are concerned in the present paper.

In most wild-caught red foxes there is no pure white on the under parts, although in some there may be small patches in the breast or inguinal regions; and the extent of the white tail tip is variable. Ranch-raised foxes, on the other hand, often have considerable pure white on the underline and on the feet, and it may extend up on the sides in the flank region. In others there may even be a white blaze on the face and a more or less complete white collar on the neck. This last condition is characteristic of two types now rather extensively raised, the platinum silver (or platina) and the white-marked silver.

Because of the cost of conducting breeding experiments with foxes, and particularly the high individual commercial value of some of the types, we have had to depend for our data on records obtainable from regular commercial ranches. We have made extensive use of such records only where we have been able to copy them at first hand and to consult with the breeder as to his standards of classification and similar points. We have confidence in the soundness of the findings on the main facts of inheritance presented but realize the data are not sufficient to establish fully some of the suggestions regarding the genetic relationship of the several characters discussed. It is hoped, however, that these suggestions may serve as a guide for further observation, and particularly for critical matings, on which we have at present only meager data or none at all.

The Platinum Silver Fox[2]

The "black" fox long had such a hold on the trade that other color phases were neglected. When they did occur they were usually disposed of summarily as indicating lack of purity in the standard stock. In 1938 Tuff, in a

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general discussion of the inheritance of color phases in foxes, described a new type being raised in Norway,

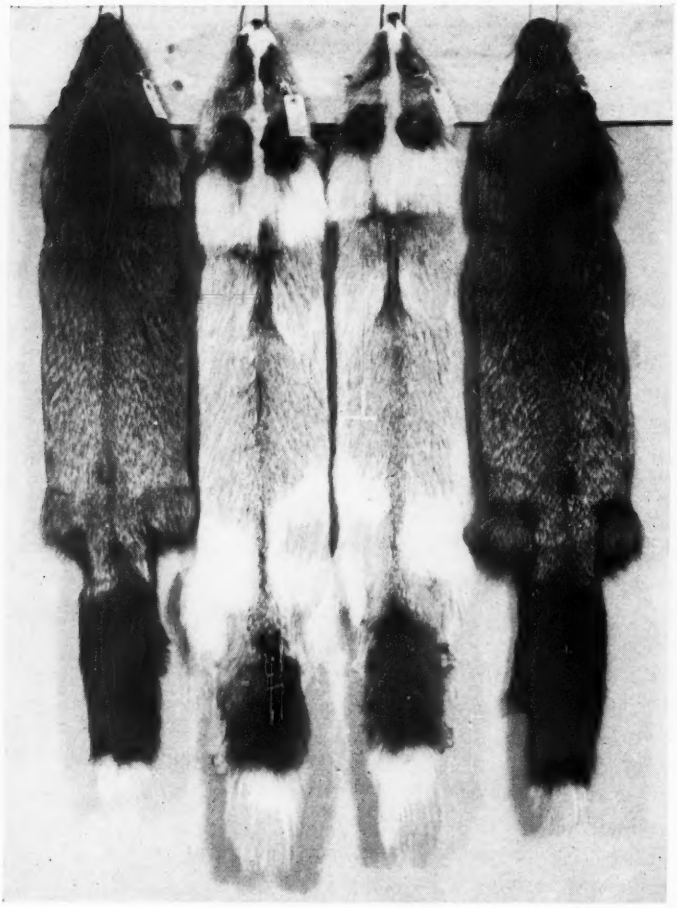

FIG. 1. Two full silver pelts (outside) and two platinum silver pelts (middle), showing the distribution of white and dilution of the black in the latter.

which he referred to as "the platinum character in the silver fox"; and the following year Mohr and Tuff (1939)

presented a fuller account, together with a discussion of the inheritance of the character. Since the appearance of the Norwegian "platina" or platinum is rather fully described and illustrated in the excellent report of these authors, a more general description will be sufficient for present purposes. The general color of the platinum is lighter than that of the silver (Fig. 1), this being due not only to the fact that there is a smaller pigmented area, but also that the black appears dilute, with a grayish or bluish tone. The actual shade varies greatly in different individuals (Fig. 2), due in all likelihood to different associated factors. Extremely light silvers often closely resemble platinum, but any one familiar with them can readily distinguish the two at all ages by the lighter tone of the black. This is particularly evident on the ears, which are deep black in the silver, whereas they may be described as a medium gray or mouse-color in the platinum. The young pups are even easier to distinguish, as the young platinums are dull bluish while the silver pups are at first definitely black, only later acquiring the silvering which makes them appear lighter.

The most characteristic thing about platinum is that it is always accompanied by a considerable amount of white spotting. Mohr and Tuff have well described it as follows: "White snout, a blaze along the nose and forehead joining with a white collar around the neck. The breast and a broad stripe on the belly are white and the same is true of the legs and the distal part of the tail. The size of the markings is somewhat variable, particularly on the legs, and the white collar may be lacking in dark individuals." As they add, in the white markings on the nose and legs there are as a rule small black spots, but these are not of the deep black color that they are when they occur in silvers. As a matter of fact the amount of white on the face may in some cases be so small that the classification by phenotype might be doubtful as an index of genotype if it were not for the other characteristics of the platinum.

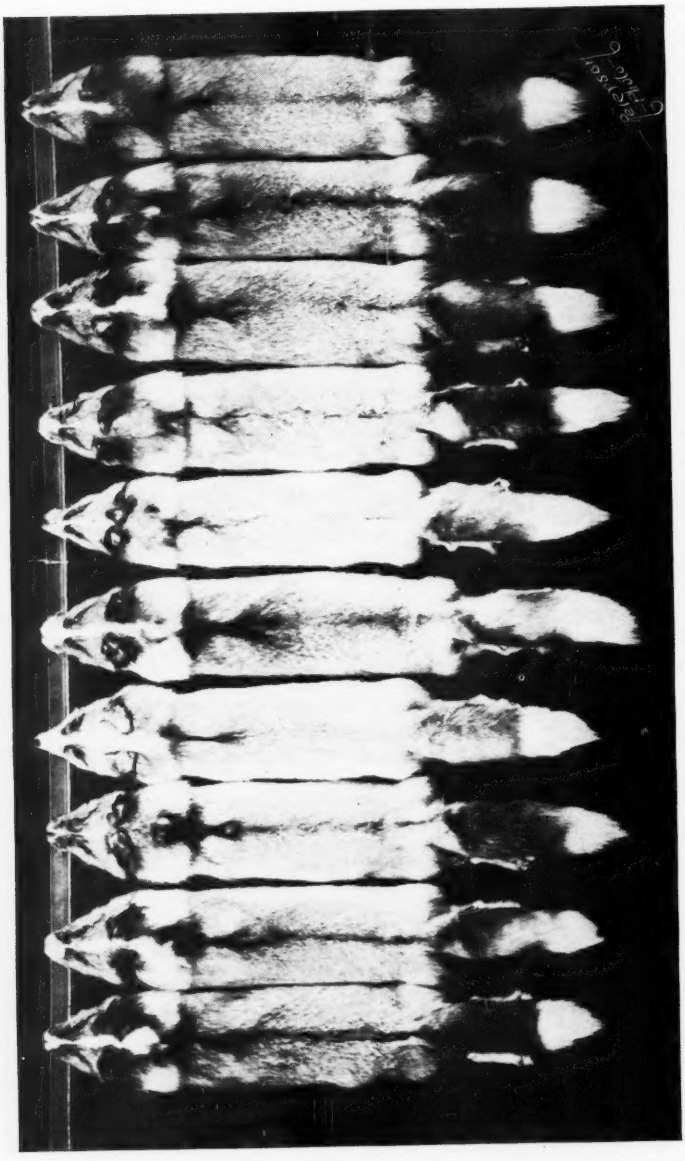

FIG. 2. Display of platinum silver pelts showing some of the variability in this color phase. More extreme examples occur, both with respect to amount of white and shade of color, than are here represented.

The Norwegian platinums are, for the most part at least, descended from a single mutant male known as "Mons," which appeared in 1933 in a litter of six pups from a long line of silver ancestors originally imported from Canada. Brager-Larsen (1940) says it was considered "a freak silver fox," which of course it really was. In the following year, 1934, one of the silver grandmothers of "Mons" gave birth by a different male to a litter of six pups, one of which appeared to be a typical platinum. This was a female, known as "Bergetta," and while it is not stated definitely it is presumed that her descendants have added to the Norwegian platinum stock. At the time Mohr and Tuff wrote, the "Mons" and the "Bergetta" descendants had not been interbred, so the authors cautiously refrained from stating whether the mutations were the same. It is interesting and possibly significant that these two mutants appeared in the same line of descent. There appears nothing else unusual in the pedigree of "Mons" except that "white markings" are noted as having occurred three or four generations back on the paternal side. There is relatively little inbreeding evident in five generations back, but this would not be necessary to bring out a dominant, which these appear to be. Two or three other somewhat similar and independently occurring mutations are mentioned. Little is known of these, but examination by Mohr and Tuff of one known as "7K" convinced them that it was distinct from the "Mons" type. It is possible this may have been of the white-face silver type discussed later in this paper.

Mohr and Tuff point out that the breeding records they had clearly indicate that platinum is an ordinary dominant, not sex-linked, and that the homozygous type was unknown. This was not surprising, considering that most of the platinums were from matings of platinum $\times$ silver. Such matings gave results approximating very closely the expected 1:1 ratio of platinum and silver offspring. The few available matings of platinum $\times$ platinum, however, gave more nearly a 2:1 ratio than the

3:1 ordinarily expected from the pairing of heterozygotes. To explain this the authors suggested the possibility that the dominant platinum gene may be lethal in homozygous condition. As will appear later, our findings support this suggestion.

According to Brager-Larsen (1940) Mr. Kjaer, who had bought "Mons," in 1936 marketed the first platinum pelt at the Oslo sales for $200. The following year nine platinum pelts were offered and bid in for a Buenos Aires retailer, bringing as high as $500 for a single pelt and an average of $300. This favorable reception led to the formation of the Norwegian Platinum Fox Breeders' Association and a boom in prices of platinums and for matings of platinums to silvers ensued. It is stated that the usual price for matings was better than $1,000. The craze for platinum continued and it is reported that when, on January 22, 1940, a large part of the 1939 output from Norway was sold in New York, one skin brought a world record price of $11,000! The publicity resulting from this sale naturally concentrated the attention of American breeders on the new color phase and changed their attitude toward new colors in general. The Norwegian breeders placed an embargo on the exportation of platinum breeding stock, but it was soon apparent that there were already in North America at least three independent sources of mutations which were very similar to if not identical with each other and with the Norwegian platinum. It is true that any one thoroughly familiar with them can often tell to which strain a particular animal belongs but this is doubtless because of different accompanying minor factors which serve somewhat to characterize the different strains. For present purposes the description of the Norwegian platinum already given will suffice equally well for the American. Minor differences will be mentioned in connection with the strains, which have come to be generally known from the ranch on which each was developed and publicized and not necessarily by that on which the mutation first occurred.

The Corbin and Werth Strain

The mutant from which this strain was developed was born in 1937 on the Hillcrest Fox Ranch of Mr. Guy Corbin near Mount Horeb, Wisconsin. It was one of a litter of ordinary standard silver foxes. There was nothing unusual in the ancestry of this litter, and the only known inbreeding in the pedigree was that one individual appeared as both the maternal grandfather and the paternal great-great-grandfather. The mutant was named "Hillcrest Chief," and is still alive (1942). In 1938 he was mated to a silver paternal aunt, named "Ruby," resulting in a litter of 2 platinum and 2 silver pups. This indicated that Hillcrest Chief is heterozygous, and subsequent breeding history has, as in the case of the Norwegian platinums, failed to disclose a homozygous platinum. Of the platinum pups, one was a male, which was given the name "Stagehand"; the other a female called "Sunbeam." The following year, 1939, Hillcrest Chief

Fig. 3. Platinum silver fox. Photographed on Capitol Fox and Fur Ranch, Madison, Wis.

was mated polygamously to five Corbin silver females and to one silver female belonging to the Capitol Fox and Fur Farm of Madison, Wisconsin. In the same year Stagehand was mated to a silver littermate and to a Capitol silver female. Sunbeam was mated to an unrelated silver male. These nine matings produced an aggregate of 22 platinum (14 males, 8 females) and 15 silver pups (5 male, 9 female, 1 ?). Six of the platinums were from the two Capitol females and this ranch bought also four of the other platinum males.

TABLE I

SUMMARY OF BREEDING RECORDS OF WERTH AND CORBIN PLATINUM SILVER AND SILVER FOXES (1938–1942)

Parents	Offspring			Total pups	No. of litters	Average litter size
	Platinum	Silver	White			
Silver × silver	0	1,215	0	1,215	267	4.6
Platinum × silver	434	418	0	852	191	4.5
(Expected—1 : 1)	426	426	0			
Platinum × platinum	12	8	3	23	11	2.1
(Expected—2 : 1 : 1*)	13.3	6.7	[6.7]			

* Calculated on the number of pups in the two viable classes.

Our association with the subsequent breeding of the platinums of this strain has been rather close, as Mr. John Werth and his son Anton, owners of the Capitol Fox and Fur Farm, have not only generously placed all their breeding records at our disposal but have made numerous matings suggested by us for their genetic interest and have given us access to their plant at all times (Fig. 3). This has afforded us opportunity for frequent consultation and for observation of the litters produced and their later development. Table I summarizes the available data on platinum matings in this strain. They include all the matings involving platinum on the Werth ranch and a few from Corbin's. The matings (191) of platinum × silver have produced 434 platinum and 418 silver pups, which is a reasonably close 1:1 ratio, and is in

accord with Mohr and Tuff's results for the Norwegian platinum (96 platinum to 88 silver).

Mohr and Tuff reported 22 platinum and 10 silver offspring from mating of platinum × platinum and point out that this "approaches a 2:1 ratio instead of the expected 3:1." It was from this that they suggested that the homozygous platinum might be lethal. We have records on 11 litters from mating of platinum × platinum, with results as shown in the lower part of Table I. These results differ from those of Mohr and Tuff in that in addition to platinum and silver pups there were three that were *completely white*. This suggests that these white pups may represent the homozygous class, which usually dies at some early stage but from which an occasional pup may survive to birth or a little longer. For this reason these white individuals deserve further consideration.

The three white pups all came from the same platinum female mated successively in three years to the same platinum male.[3] The results of their litters is as follows:

1940, 1 platinum: 0 silver: 1 white;
1941, 0 platinum: 0 silver: 1 white;
1942, 1 platinum: 0 silver: 1 white.

Each of these white pups was entirely white with blue eyes. The one born in 1940 was not discovered until the nest box was examined when the litter was about three weeks old. It was alive and seemed to be doing well (Fig. 4) up to about five weeks of age, so was left with its mother. Then one morning all that was found was its tail; it had either died or been killed and eaten by the mother. The 1941 white pup lived to at least 28 days, but when it was to be taken out for "pilling" on the 30th day no trace of it was to be found. In view of the past experience, this female was watched closely at whelping time this year, for it was planned if there was another

[3] There is a possibility, though it is unlikely, that the mating was by a different platinum male in 1942. This, however, should not change the expectation.

white pup to remove it at once and attempt to raise it either by hand or with a cat as foster mother. The female whelped two pups on March 24, 1942, a platinum and a white. The white was only about half the size of the other and was apparently dead at birth; otherwise it appeared normal (Fig. 5).

The question may be asked, if the silver and the white represent the respective homozygotes, and platinum the

FIG. 4. Completely white pup, 24 days old, from platinum × platinum mating. Lived to about five weeks of age. Capitol Fox and Fur Ranch. This picture was first published in *American National Fur and Market Journal*, Vol. 18, No. 12, July, 1940.

heterozygote, why the ratio from platinum × platinum matings in general should be so far from 1:2:1. This may be in part due to chance—the available numbers are small—and probably a good deal to a differential death rate before the litters are observed. Pups that die in the nest box may be eaten by the mother and as the litters on most ranches are usually not disturbed until they are about three weeks of age, any pup which died before that

time would be likely to be unrecorded. It is more than likely, for example, that if special care had not been taken to look for it the 1942 white pup would not have been seen at all. Furthermore, the fact that the white pups the two preceding years lived for an appreciable time would appear to be quite unusual, due perhaps to the individual physiology or behavior of this particular female. It is quite possible that the homozygous pups ordinarily die at some time during fetal development and that live birth is a rare event. The small average litter size (2.1) of the

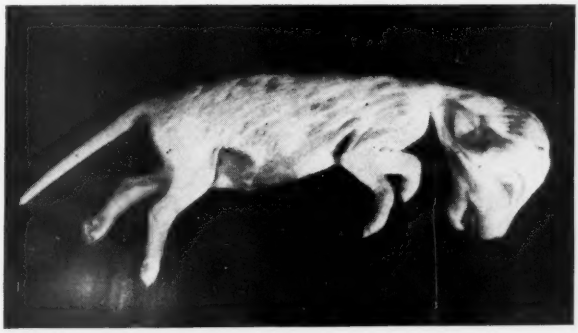

FIG. 5. White pup from platinum × platinum mating. Dead when found. Capitol Fox and Fur Ranch.

platinum × platinum matings as compared with that from platinum × silver (4.5) is further evidence of some reproductive disturbance, and premature death seems a plausible explanation. The reduction in this case is more than could be accounted for by elimination of one fourth of the offspring, but the numbers are too small to make further speculation profitable. The platinum × silver average compares favorably with that of 4.6 in the silver × silver matings on the same ranch and during the same period. Kellogg (1941) has tabulated data from another Wisconsin ranch showing a total of 2,997 pups in 638 silver × silver matings. This is an average of 4.7 and indicates that not only are the Werth foxes represen-

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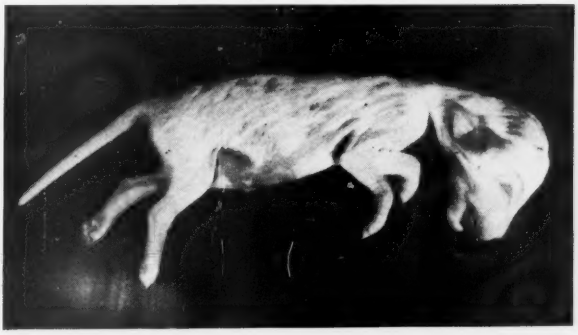

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tative in this respect but that mating of platinum to silver does not appreciably affect the litter size.[4]

Much variation is found among the platinum foxes with respect to the extensiveness of the white markings and the intensity of pigmentation or depth of shade on the colored portions of the pelage. The white markings, wherever they appear, may lack symmetry, white often extending up only one side of the neck rather than forming a complete collar or extending equally on both sides. The white tip of the tail is characteristically larger than in regular silvers, and there may be considerable white extending up on the flanks. Very light individuals do not necessarily have more extensive white markings, while dark ones may show much white. The darker platinums, however, appear to show more dark spotting in white areas than do the lighter ones. It is possible that some of this variability is non-genetic, but it is more probable that much of it is determined by factors in the silver foxes to which the platinums are bred.

For a conclusive test of whether platinums may ever be homozygous, a considerable number of platinums from platinum $\times$ platinum matings should be bred to silvers. This test is seldom made by breeders. They would like to secure a strain of true-breeding platinum and some have the idea that platinum offspring from two platinum parents should have the character "concentrated" and hence themselves produce a larger proportion of platinums. Not only has this not proved to be the case but it is not in accord with genetic expectation. Only one of the Werth platinums produced in this way in 1941 was tested and she produced both platinum and silver pups in 1942.

THE CODY STRAIN

A brief history of this strain of platinum foxes has been given by Mr. W. A. Granquist (1941). In 1937, according to his report, the mating on the Buffalo Bill

[4] It should be kept in mind that these are not "ranch averages," as they apply only to certain classes and do not include infertile matings.

Fur Farm, at Cody, Wyoming, of a full silver standard male, M 125, with a three-fourths silver female, F. M. 38, gave a litter of four pups, three of which were normal silver and one, a male, was recorded as a pup as "almost white." This individual was named "America" and the Cody platinums are all descended from him. His ancestors had been on the farm since 1928 and were all standard silvers; furthermore, his parents produced four subsequent litters, all silvers. The breeding from "America," as compiled from the Granquist paper, is summarized in Table II. It will be noted that the essential equality of platinum and silver offspring corresponds to what has been found in other matings of this type.

The La Forest Strain

The foxes which have come to be generally known as La Forest platinums are again descended from a single mutant individual. The strain has been developed by Dr. J. E. La Forest of Quebec, Canada, who has put on record a brief account of its origin and development (La Forest, 1941). In 1938 a male "freak" platinum was born on the ranch of a neighbor. The parents were registered silvers and had previously given four litters, all silvers. They were mated again in 1939, hoping for another platinum, but the litter was all silvers.

The platinum "freak" produced thirteen pups in 1939. The number of litters and the proportion of silvers to platinums are not given, but it is stated that there were "two full litters of pure platinums." One interesting mating was of the original platinum to a white-marked silver, that is, she was a silver with a white spot on the neck and also white spots between the front and between the hind legs. This mating produced two platinums, one silver with white markings like the mother, and one plain silver. The two platinum pups, a male and a female, were very largely white-marked, with hind legs full white and the white extending "all over the back, blue eyes, pink nose, pink feet and claws." The objective is to

obtain light, even color in the platinums, and it was a disappointment when "the mating of an extra pale platinum male, with blue eyes and pink nose, to his half sister of the same quality and color . . . produced a litter of very nicely marked pups, but of very dark color with dark underfur, and of rather poor quality." This emphasizes again the considerable independence of these variable characters.

Judging from the appearance of the animals and from the breeding history it would seem probable that the La Forest platinums are genetically like the two other American strains and the Norwegian. Dr. La Forest, it is true, makes the general statement that his matings of

TABLE II

EARLY HISTORY OF PLATINUM BREEDING ON THE BUFFALO BILL FUR FARM, CODY, WYO., 1937–1939. (COMPILED FROM GRANQUIST, 1941)

Year	Mating	Offspring	
		Platinum	Silver
1937	"America" × silver full sister (F. A. 61)	2*	2
1938	"America" × silver full sister (F. A. 61)	1	2
	"America" × silver (F. A. 23)	1	2†
	"Young America" × silver (F. A. 141)	2	3
1939	"Young America" × silver (F. A. 23)	4	2
	A mating of "America" to a platinum female produced no pups		
	Total—platinum × silver	10	11

* One, a male, named "Young America"; other died.
† The number in this litter is not definitely stated, but the statement is made that it was a "similar litter" to the one immediately preceding.

platinum to platinum "produced just as high and as healthy litters as any other matings of platinum to silver" and that the percentage of platinum pups is about the same, but no data are presented. Of course, the genetic identity of these various platinums can not be definitely proven until controlled matings between the different strains can be made.

Platinum foxes with pink or spotted noses and with one or both eyes partly or wholly blue are not uncommon. This condition is quite obviously correlated to a considerable extent with the general amount of white on the animal and is not separately inherited.

White-marked Silver

The striking thing about the true platinum or platinum silver just discussed is that this color phase is always accompanied, genetically, at any rate, by white markings, which are usually more extensive than the small ventral spots and white tail tip of the silver. On the other hand, there are foxes which have the white blaze and other white markings similar to the platinum, but which otherwise are like ordinary silvers. These foxes are variously known among breeders as "white-marked silvers," "white-face silvers" and "ring-necks," depending on the

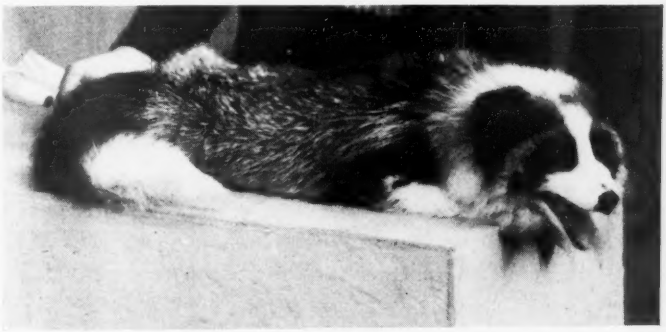

Fig. 6. White-marked silver fox. Photograph from Mr. Bruno Delsman, Hartland, Wis.

extent and location of the white (Fig. 6). Because of the resemblance of the white markings to those of the true platinums, the lighter colored specimens are often confused with platinums and pass as such, or they may be called "platinum-type silvers." There is no question that they sometimes are phenotypically very similar to platinum, the resemblance between the two types extending even to the frequent occurrence of blue eyes when there is a large amount of white (Fig. 7). But our examination of many animals of these types convinces us that the differences we previously outlined as distinguishing silver from platinum, particularly the shade of color

FIG. 7. White-marked silver fox with left eye blue, right eye normal. Photographed on ranch of Russell Colpitts, Salisbury, N. B.

in the young (Fig. 8) and of the ears in the adults, serve in this case to class these foxes as being really unusually light silvers on which the characteristic white-face mark-

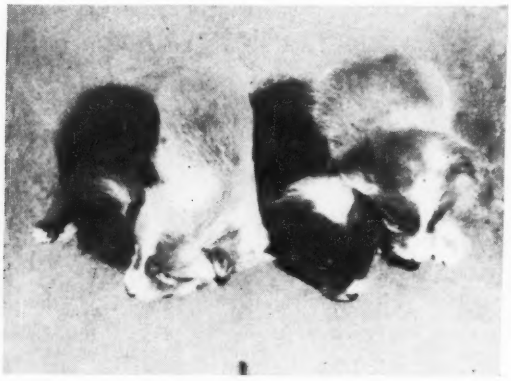

FIG. 8. Two white-marked and two platinum silver pups about three weeks old, showing contrast at that age. Photographed on Capitol Fox and Fur Ranch.

ings have been superimposed. Combined with this may be another characteristic consisting of white hairs, not barred, sprinkled through the pelt, similar to the "silvering" sometimes found in rabbits and mice. To distinguish it from the silver character in foxes, we have termed it roaning. It is variable in amount but apparently increases with age. When present in considerable degree it lightens the pelt appreciably and increases the superficial resemblance to true platinum. Whether roaning is entirely independent of white face in its inheritance is not known.

Regarding the origin of white marking, Mr. Harry J. La Due (1937) says: "White spotting in silver black foxes occurred early in the industry but most breeders quickly eliminated such animals from their herds. They were first noted in Canada and then in some of the old-time herds around Muskegon, Michigan. The wide distribution of breeding stock from these old herds has caused the appearance of white spotted foxes in many places in the United States." He elsewhere (1929) speaks of these Muskegon foxes as being "spotted like Boston Terriers."

It is probable that this mutation has occurred independently a number of times, but information as to its independent origins is scanty. The fact that different strains are recognized, such as the Colpitts, the McNeil, the Garvey or the Holman white-faces, is not evidence that each has descended from a separate mutation, but certainly some of them have. The Colpitts mutation is said to have originated in Calgary in 1928 (Avery, 1941).

The Springborn or Kaempf foxes apparently arose from an independent mutation. According to Mr. W. J. Boston (1942), the Wausau Silver Fox Ranch, Inc., in 1929 sold some silver foxes to Ed. Springborn of Shawano, Wisconsin. The following year Mr. Springborn complained that one pair had thrown, in a litter of four, "a pup that looked like a collie dog." This "freak" was taken back by the Wausau ranch and was

registered in the American National Fox and Fur Breeders Association under the name "Wausau Sport E," and tattoed W.W.–E 196. The interesting thing about this individual was that his coat was "sprinkled quite profusely with white hairs." The white-face character seemed to breed as it does in other cases, but it is stated that part of the white-face progeny had this characteristic of acquiring white hairs and lightening up when about two years of age, whereas the others did not; nor did the plain silver segregates develop this character, which presumably is the roaning previously mentioned. The individuals with the character are said to develop into a beautiful pastel shade of blue gray and are given the fancy name of "pastel platina silvers."

BREEDING OF WHITE-MARKED SILVER

A significant thing in the breeding of white-marked silvers is that, as is the case with platinum, apparently there is no evidence that they are ever homozygous for the character—matings of white-marked to plain silver always produce these two types in approximately equal numbers. While this is the regular experience of breeders, our definite and, we believe, reliable records in support of it are limited to a few sources. Those cases in which we have been able to copy down the litter-by-litter records are summarized in section (a) of Table III. The grand total of 282 white-faces to 241 without white faces is reasonably close to the expected equality if the white-face parents were all heterozygous. This is, of course, only indirect evidence that the homozygous condition is nonexistent among breeding animals, but two other bits of evidence point towards the same conclusion.

It will be recalled that the mating of platinum to platinum resulted in greatly reduced litter size, which was ascribed to prenatal or neonatal lethality of the expected homozygous "platinum" pups. Section (b) of Table III gives indication of a similar situation in the mating of white-marked $\times$ white-marked, the resulting 183 white-

marked to 79 silver pups being nearer a 2:1 than a 3:1 ratio. Even more significant is the reduction in average litter size, the drop from 4.6 to 3.3 corresponding almost exactly to the expected if one fourth of the offspring are eliminated. The conformity of these results in the data from different sources is striking.

Still further evidence of the similar behavior of white-face when associated with silver and when associated with platinum is furnished by the appearance of pure white

TABLE III

SUMMARY OF MATINGS OF WHITE-MARKED TO STANDARD SILVER* AND WHITE-MARKED TO WHITE-MARKED FOXES

Source	Offspring		Total pups	Total litters	Average litter size
	White-marked	Standard			
(a) *White-marked × standard silver*					
McIlquham and McGill (1941)	20	14	34	9	3.8
Fred C. Beck (1941–42)	86	78	164	36	4.6
Sanford Colpitts† (1941)	157	132	289	60	4.7
Capitol Fox and Fur Farm (1942)	19	17	36	8	4.5
Total	282	241	523	113	4.6
(Expected—1 : 1)	261.5	261.5			
(b) *White-marked × white-marked*					
Sanford Colpitts (1941)	164‡	72	236	71	3.3
Fred C. Beck (1941–42)	19	7	26	8	3.3
Total	183	79	262	79	3.3
(Expected—2 : 1)	174.6	87.3			

* Some other color types, such as "pearl platinum," have been included since they are independent of white marking and in relation to it behave the same as standard silver.

† There may be included here a few matings of Strain B white-marked, to be discussed later, but this should not change the ratio expected.

‡ Three of these pups were classed as white-eared; discussed in a later section.

pups in matings of white-marked to white-marked as shown in the first section of Table VI. These two matings are not included in Table III because they are selected from the records on other ranches. We had opportunity to examine the one white pup on the Russell Colpitts ranch as it had been preserved in alcohol and it appeared in all respects similar to those produced in the platinum matings (Table I and Fig. 3). The four white pups in one litter on the Curtis-Davis ranch happened to

be found because the mother had trouble in whelping. All four were naturally bobtailed.

RELATION OF WHITE-FACE (WHITE-MARKED) SILVER TO PLATINUM SILVER

It has been shown that platinum and white-face are practically identical phenotypically with respect to the white markings. They also correspond in that both apparently exist only as heterozygotes, that reduced litter size in heterozygote $\times$ heterozygote matings suggests homozygote lethality, and that completely white pups, dead at birth or soon after, are occasionally produced in both types. The only constant difference is that the black pigment appears to be more dilute in the platinum. The question naturally arises as to whether these are two separate and independent mutations, involving different loci on the same or on different chromosomes or whether white-face and platinum are alleles and both allelic to silver (non-white-marked). Unfortunately the reliable evidence bearing on this point is scanty but seems of sufficient interest to present (Table IV). The genes for platinum and white-face might be symbolized as P and W, respectively. If they are independent, with free segregation, the mating of platinum to white-face would be expected to give offspring in the ratio of 2 platinum: 1 white-face: 1 silver. This is on the assumption that the genotype with both P and W is not lethal except when one or the other is homozygous. On the other hand, if white-face and platinum are allelic, in the order of dominance $w^+ \rightarrow W \rightarrow W^P$, the expected ratio from the above mating would be 1 platinum: 1 white-face: 1 silver, the WW^P combination being lethal. The results from three such matings, 7 : 6 : 5, approach this latter ratio but are insufficient to be critical.

The real test of the two hypotheses lies, of course, in the breeding of the platinum offspring from the platinum $\times$ white-face cross to silvers. On the assumption of independence, half the platinum offspring when mated to

silver should produce all three classes of pups in the ratio of 2 platinum: 1 white-face: 1 silver, and the other half only platinums and silvers, in equal proportions. Assuming triple alleles, all the platinums from the first cross should produce only platinum and silver offspring, and in equal numbers. We have definite record of only one animal so tested—a male produced on the Werth ranch in 1941. Bred to three silver females he produced 9 platinum, 10 silver and no white-face.

TABLE IV

MATINGS INVOLVING PLATINUM AND WHITE-FACE SILVER

Source	Offspring			Total pups	No. of litters	Average litter size
	Platinum	White-face	Silver			
Platinum × white-face						
Ekstrom (1942; *teste* Werth)	2	4	1			
Werth (1941)	2	0	3			
Fred C. Beck (1942)	3	2	1			
Total	7	6	5	18	3	6
(Expected on multiple allele hypothesis—1:1:1)	6	6	6			
(Expected on independent gene hypothesis—2:1:1)	9	4.5	4.5			
Platinum ♂ (from Werth mating above) × 3 silver ♀♀						
Werth (1942)	3	0	4			
	4	0	3			
	2	0	3			
Total	9	0	10	19	3	6.2

The litter size in all these matings is surprisingly high even if no genetic lethal were concerned. There is certainly no obvious reason why it should be above that of ordinary silver × silver matings. Moreover, in the matings of platinum × white-face, death of one fourth of the pups would be expected on the multiple allelic interpretation, and in so far as the litter size in these three matings has any significance it would seem to favor the idea of independence. The number of litters concerned, however, is too small to carry much weight.

Without decisive evidence either way we are inclined to adopt provisionally the multiple allelic interpretation as being on the whole the simpler. Independence would

involve two loci, at one of which mutation occurred to produce white-face and at the other a mutation producing both white-face and dilution of black, giving the platinum. The allelic interpretation would furnish a plausible explanation of the fact that platinum is always accompanied by white-face—the white-face mutation is a first step and platinum a further one, involving dilution. Without

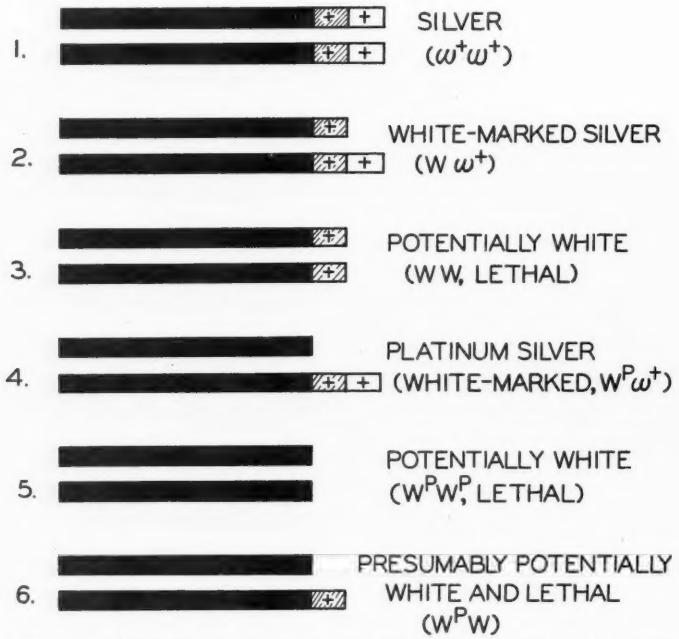

FIG. 9. Diagrammatic representation of chromosome types on deficiency hypothesis. Symbols in parentheses indicate the phenotypic effect of the assumed deficiency.

commitment as to the actual mechanics involved, this might be represented diagrammatically as a progressive deficiency (Fig. 9). As depicted, the bars at the top (1) represent the normal wild-type chromosomes, producing a silver fox, with a normal gene for self-color in the right-hand terminal section and one for intense black pigment in the section next to it. A unit break at the right end

results in white-face (2) and is lethal if homozygous (3). A second break (4) produces platinum, and of course white-face, and this would also be lethal when homozygous (5). In every case, for a fox to be viable one of the pairs of chromosomes must be complete. These assumptions are sufficient to account for all the known breeding facts. On this interpretation a deficiency (absence) produces a dominant effect; many cases of this sort are known.

Two Factors for White-marking

On the Sanford Colpitts ranch we were shown a striking type of white-marked fox we had not observed elsewhere,

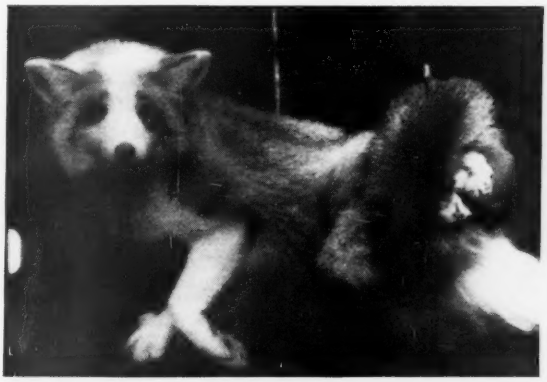

Fig. 10. "White-ear" fox on the Sanford Colpitts ranch, Salisbury, N. B. Note the extension of white up the ear producing black borders and white tip.

though we had seen occasional individuals somewhat approaching it phenotypically. These animals not only have the white face and the neck ring well marked, but in addition the white extends up on the ears, particularly up the middle, producing a black border on each side and a conspicuous white tip (Fig. 10). There is considerable variation, as would be expected; the white is often unsymmetrical and may in some cases involve only one ear.

In general, however, there is little difficulty in distinguishing these "white-ears" from other white-marked foxes.

We were told that the "white-ear" character appeared from crossing two strains of white-marked silvers from different sources. These two strains are in general very similar, though as they occur on that ranch one can usually be distinguished by a characteristic triangular white marking on the neck at the base of the skull. This area is usually not white in other white-marked silvers, or in platinums, unless it is included as a part of a complete or incomplete collar. Both these strains will be referred to collectively as white-marked, but since they appear to be fairly distinct and to have a complementary action, increasing the amount of white and producing white-ears when crossed, the regular type may be designated Strain A and that characterized by the triangular spot as Strain B. For brevity, as heretofore, the plain silvers (without white markings) will be referred to simply as silvers, although, of course, all these types show silvering in the pelt.

The breeding results with white-ear shown in Table V support strongly the breeders' idea that white-ear is different genetically from white-marked. If it were due to the same gene as white-marked, influenced perhaps by modifiers for extension of white, mating of white-ear to silver should give a 1:1 ratio when white-ear and white-marked offspring are combined. The numbers obtained, 196 to 89, differ significantly from equality and suggest that Strain B may depend upon a different gene for white-face, similar to W in its phenotypic manifestation and in being lethal when homozygous, but located at some distance from it, presumably on a different chromosome. This Strain B gene may be designated as W_{II} and its normal allele as w^{+}_{II}. The further assumption is necessary that W and W_{II} have a supplementary effect such that when both are present the white is considerably extended, running up on the ears, and producing the

white-ear type, which would perforce always be of genotype $Ww^{+}\ W_{II}w^{+}{}_{II}$.

The results of the available matings shown in Table V may now be examined on the basis of these assumptions. Mating of white-ear to silver should by formula produce 1 white-ear: 2 white-marked: 1 silver. The obtained 55:141:89 deviates considerably from this expectation but still has a probability of .05–.01 that the deviation is due to chance. No deaths from genetic cause are expected in this cross and the average litter size of 4.7 indicates that such have not occurred.

In the mating of white-ear × white-marked, shown in the lower part of Table V, expectation is that genetic

TABLE V

MATINGS INVOLVING STRAIN A AND STRAIN B WHITE-FACE (DATA FROM SANFORD COLPITTS RANCH, 1941 SEASON)

Parents	Offspring			Total pups	No. of matings	Average litter size
	White-ear	White-marked	Silver			
White-ear × silver	55	141	89	285	60	4.7
	196		89			
(Expected—1:2:1)	71.25	142.5	71.25			
(Expected—1:1)	142.5		142.5			
White-ear × white-marked	38	62	18	118	34	3.5
(Expected—2:3:1)	39.3	59.0	19.7			

lethality would remove one fourth of the pups and that the remainder should appear in the proportions of 2 white-ear: 3 white-marked: 1 silver. The obtained result of 38:62:18 respectively in these classes is uncannily close to this expectation, but the phenotypic classification as we copied it down had already been made by the breeder on the young pups without any thought of genetic theory. Equally striking is the fact that the average litter size is reduced almost exactly one fourth from that of the white-ear × silver (4.7 to 3.5).

Mention was made in the discussion of platinum that some individuals have one or both eyes partly or wholly

blue, particularly when there is a large amount of white on the face. The same is true of the white-marked silvers and blue eyes are even more prevalent in the white-ear foxes, in which there is usually an even greater extension of white. Furthermore, the white-ear foxes as a group appear to be more nervous than the other classes; this is manifested in greater activity and sometimes by a habit of throwing the head backward and to one side. A few individuals exhibited circus movements, somewhat like those of the waltzing mouse.

WHITE PUPS IN WHITE-MARKED AND WHITE-EAR MATINGS

Our records of completely white pups from platinum × platinum matings were presented in Table I and discussed in that section. In Table VI are presented data of five litters involving white-marked and white-ear which produced a total of nine white pups similar to those from the platinum matings, except that none of these was alive when found.[5] It was the opinion, however, that some of them at least were alive at birth as they had sand inside the mouth, whereas it probably would not have got in so far if they had been dead.

The five white pups from the white-marked × white-marked matings have already been discussed (p. 309). The numbers in the other matings are too small to make a discussion of the ratios profitable further than to point out that on the basis of the genetic interpretation suggested lethality would be expected in both types of matings. In the white-ear × white-marked mating one fourth of the pups would be expected to fall in the "prenatal lethal or white pup" class, while in mating of white-

[5] In *Canadian Silver Fox and Fur* for July, 1942 (Vol. 8, No. 7, p. 5), is the picture of a white pup from the mating together of "two ring-neck animals" which were half-sister and half-brother. The pup lived to five weeks of age and appears from the photograph and description in all respects similar to the white pups reported in this paper. This case occurred on the ranch of Mr. Lowell W. Hancock, of Prince Edward Island, and was reported by Dr. C. K. Gunn, director of the Dominion Experimental Fox Ranch.

ear × white-ear the expectation would be nearly half (seven sixteenths) in that category.

Mohr and Tuff stated that the Norwegian platinum character is not sex-linked. We have found the same to be true in this country; and this applies as well to white-marked. The records do not include the degree or extent of the white markings, hence we have not been able to grade individuals and classify them with respect to sex. It is our impression, however, and we have encountered

TABLE VI

SELECTED MATINGS INVOLVING WHITE-MARKED AND WHITE-EAR WHICH PRODUCED COMPLETELY WHITE PUPS

Parents	Offspring				Total pups	No. of litters	Average litter size
	White-ear	White-marked	Silver	White			
White-marked × white-marked	0*	2	1	1	4		
	0†	1	0	4§	5		
Total	0	3	1	5	9	2	4.5
White-ear × white-marked	1‡	2	1	1	5	1	5.0
White-ear × white-ear	0‡	0	0	2			
	1†	1	0	1			
Total	1	1	0	3	5	2	2.5

* Russell Colpitts Ranch.
† Howard Colpitts Ranch.
‡ Curtis-Davis Ranch.
§ All four naturally bobtailed.

no opinion to the contrary among breeders, that the white-face character is expressed equally in both sexes.

Throughout the records there appears to be a tendency for an excess in the classes having white markings over the plain silvers. This is true both in the platinum (Table I) and the white-marked (Table II). In the case of the latter it might conceivably be due to faulty classification of some of the borderline phenotypes, but this explanation would not apply to the platinums. At present we have no other explanation to offer.

SUMMARY

(1) Platinum silver, the platinum color phase in silver foxes, first brought to attention by Norwegian breeders,

appears to have arisen independently by mutation in at least three instances in the United States and Canada.

(2) The platinum character is characterized by a dilution in tone of the black pigment in the coat, accompanied by white markings, particularly on the face and neck, which are usually fairly extensive.

(3) Platinum behaves in inheritance as a dominant which is lethal when homozygous. This is supported by the fact that only heterozygous individuals are known and the further fact that the litter size is reduced in platinum by platinum matings. Completely white pups which are dead at birth or die shortly after are occasionally found. These are taken to represent individuals of the homozygous dominant class which have survived longer than is usual or by chance have been found.

(4) A phenotypically similar white-face mutation is found in the silver fox. This differs from platinum in that the tone of the black is intense, rather than dull, particularly on the ears, elbows and other places where it is not so much intermixed with white or white-banded hairs. This difference in intensity of the black is particularly diagnostic in the young pups, the platinums at that stage being bluish, the white-face silvers definitely black.

(5) Inheritance of white-face is similar to that of platinum in that the dominant homozygote is lethal, litters from heterozygote $\times$ heterozygote matings are reduced in size, and completely white pups are occasionally found in such matings.

(6) The data are insufficient to settle definitely whether the genes determining them are independent or allelic. The latter hypothesis is adopted provisionally as being the simpler, and the symbols w^+, W and W^p are adopted for standard silver, white-face and platinum, respectively, in order of dominance. The white-faces in this allelic series are denominated Strain A.

(7) It is suggested that the relation of white-face and platinum to silver might be explained by a progressive chromosome deficiency.

(8) Another strain of white-faced, or white-marked, foxes is very similar to Strain A in phenotypic appearance and seems again to have the same characteristics of

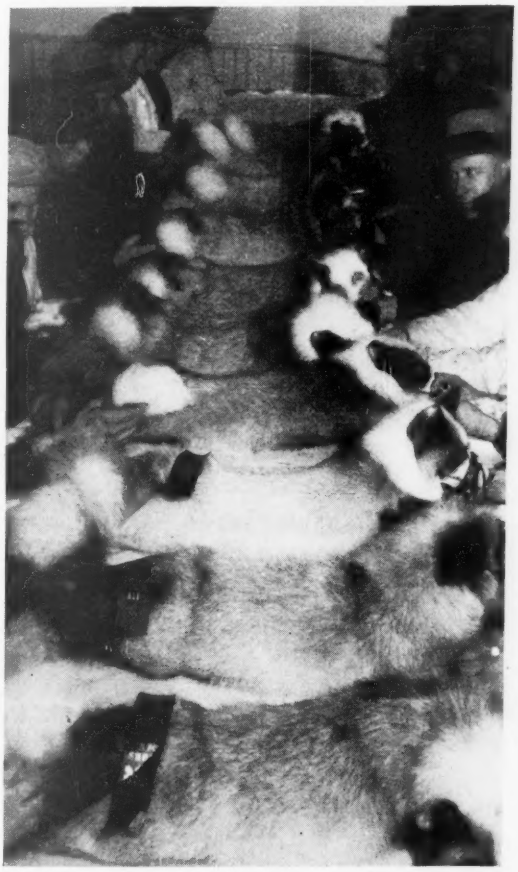

FIG. 11. Display of white-ear and white-marked foxes at a breeders' show. Photograph supplied by the Colpitts ranches, Salisbury, N. B.

inheritance. The breeding data, however, indicate that it is not an allele of Strain A, but that the gene, or possibly deficiency, responsible for it involves a different chromosome pair. This second strain we have called Strain B.

(9) Strain A and Strain B appear to be supplemental in their action, as foxes carrying genes for both have the white markings of the face and neck considerably extended. Commonly the white extends up on the ears in a characteristic fashion which has led to naming this type of foxes "white-ears."

(10) Blue eyes occasionally occur in each of the types of foxes discussed in this paper. The blue may invade the iris of one or both eyes (*heterochromia iridis*) or one or both eyes may be completely blue. In general, the greater the extent of white on the face the greater the likelihood of blue in the eyes. For this reason blue eyes occur with greater frequency in the white-ear type than in the others. The white-ear foxes also appear to be of a more nervous temperament as indicated by their actions.

(11) Platinum and white-marked are not sex-linked and appear to have equal phenotypic expression in both sexes.

ACKNOWLEDGMENTS

It would be impossible to acknowledge individually all the help we have received in the accumulation of the material for this report. Not having facilities to conduct direct breeding experiments of our own, we are forced to rely in our studies of inheritance in fur-bearing animals on the assistance and the regular ranch records of breeders. In this we have met uniform interest and courtesy and permission to use such records as were suitable to our needs. A few who have furnished material help in connection with the present report should receive particular mention. As stated earlier, Mr. John Werth, father, and Mr. Anton Werth, son, of the Capitol Fox and Fur Ranch, have not only been constantly helpful in consultation but have placed their ranch records freely at our disposition and have made for our benefit a number of matings which used facilities of the ranch and were of no direct financial advantage to them. We feel unusually

fortunate to have this opportunity at our door, so to speak. We have obtained extensive and valuable records, which have obviously been taken with care, from Mr. Fred C. Beck of Thiensville, Wisconsin, from Mr. Tom McGill of McIlquham and McGill of Packenham, Ontario, and from Mr. Sanford Colpitts of Salisbury, New Brunswick. In this connection we should mention also Messrs. Russell and Howard Colpitts and the Curtis-Davis ranch, also of Salisbury, for selected records relating particularly to the completely white pups. Finally, we should be ungrateful if we did not mention the unflagging interest and help of Dr. Walter Wisnicky, director of the University Fur Animal Research Project.

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THE HERBARIUM IN MODERN SYSTEMATICS[1]

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My favorite dictionary informs me that a herbarium is "a systematized collection of preserved plants." Perhaps wisely, it has left to the individual the task of defining for himself the function of such a collection. Standing to-day at what surely must be a crossroads in the history of the world it is perhaps wisdom on our part to ask what rôle the scientific museum—and especially the herbarium—should play in the future development of our science and its relation to the advancement of the world's culture. It is particularly fitting that we discuss these matters on this occasion.

To-day there is some unrest among certain biologists who hold that there is scarcely any need for the maintenance of herbaria—that they are little else than expensive luxuries, club-houses for doddering systematists; that they have but little function within the body of biological science and should be eliminated. Some of these even say that the systematist is so far out of touch with the actualities that the species about which he so confidently writes do not really exist—that they are no more than subjectively defined population segments based upon a few specimens lying in museum cases and therefore temporary concepts existing only in the mind of man. To these critics the science of biological systematics is a hollow shell of long-outmoded concepts which had better be forgotten. For those who may be curious, it can be said that there are many who think otherwise. And I am one of them. It is my opinion that, although often genetically and morphologically complex, species are entities capable of being subjected to exact analyses of various sorts—otherwise this would never have been written. Yet there

[1] An address delivered at the dedication of the M. A. Chrysler Herbarium, Rutgers University, April 16, 1942.

are those among us who do look upon species solely as collections of dried and dusty museum specimens to be juggled hither and thither—taken from a named pigeon-hole and slipped into one of another name—because of an indecision as to what these names should represent.

There are some, wandering as in a dark and trackless forest, who have sought solace from the pain of this indecision in a manipulation of nomenclatural categories—crying aloud that by so doing they were following the path which, ultimately, would lead us to the truth. Following their fancies, they explored each nook and cranny, setting up systems for the replacing of each sere and fallen leaf upon its twig and for following each worm-hole to its worm. But each succeeding year the trees cast down additional leaves and the worms left more holes behind them, so that those whose business it was to classify things came to think only of dead leaves and worm-holes.

They designed special cases in which to save samples of their treasures and published interminable volumes in which they argued as to who among them know most about dead leaves and worm-holes. Until finally it became necessary to set up a system of rules, not only as to what one might, or might not write about dead leaves and worm-holes, but as to the manner in which it was to be published. Thus, the system of classification—the system of names—became a Sacred Cow to be worshipped for itself. And many forgot about the green growing forest which produced the leaves and the burrowing worms which made the holes.

I shall not dispute with those, lost in a system of classification based on rules, who wish to quibble over the nature of species. They are only trying to extract the milk of wisdom from their Sacred Cow, knowing not that long since she has run dry. The least they can do is to lead her into greener pastures and leave her there until such time as her udder is replenished. They should return to a consideration of living organisms.

But, you may ask, if the systematist is to return to a study of living organisms, is this not proof that the herbarium is an outmoded institution? It is a reasonable question and should be answered.

Man early became aware of the individual objects of his environment. He also learned that objects of similar appearance had similar uses. Therefore, he set up a system of classification—a system of names—for greater ease in the retention and communication of concepts and information. The invention of the herbarium with its labeled specimens was a primary step forward in the further stabilization of these concepts and names as applied to plants. There is a tremendous social functionality to these names, for they are fundamental in so many of the arts, sciences and industries, being necessary for the intercommunication of basic information. It is therefore legitimate that we make some inquiry into the methods whereby a greater functional stability may be achieved and the part which the herbarium can play in its realization.

METHODS, CONCEPTS AND NOMENCLATURAL STABILITY

I was once chatting with a friend who is an advanced amateur field naturalist and he remarked that to him the most remarkable thing about taxonomy was the fact that two men—and reputed authorities—could "burrow through the same pile of specimens and one emerge with five species and the other with seven species and a half dozen varieties." Had one wished to discourage him in his avocation, examples of considerably greater differences of opinion could have been pointed out.

As was intimated, there is a functionality to this system of names, otherwise it would long since have been discarded. But if it is to be genuinely useful there must be some continuity, otherwise chaos results. Sensing this need, the leaders of our science from time to time have sought to establish sets of rules whereby stability of concept might be achieved. Linnaeus had his set of princi-

ples. And De Candolle, who was the real father of our present epoch, outlined his system in considerable detail. This was followed by various schools of thought, among them the proponents of the so-called Berlin and Kew rules. There were the Paris and Vienna codes; these to be followed by the American code and the more recent sets of International Rules of Botanical Nomenclature. For those who are so inclined it is an interesting and revealing diversion to bring these documents together and compare them.

Although the avowed purpose of these systems and codes was to bring stability to the nomenclature of our science, where is it? As an example, Deam (1941) has pointed out that in the first year following the publication of his Flora of Indiana it was necessary—in attempting to follow only a portion of the current and valid treatments of others—to change one per cent. of the names. Does this mean that in the not too distant future the good people of Indiana, although probably blessed with much the same floristic elements as to-day, will be using an entirely different set of names?

Nevertheless, as much as we may desire nomenclatural stability, we can not expect that the names of organisms will remain completely static. We may, I trust, disregard for the moment the impractical and scientifically useless activities of those among us who are primarily concerned with the deft art of nomenclatural juggling. Yet there is need that we keep clearly in mind that the names we use can represent no more than the state of our current understanding of those biological units we call genera and species.

Therefore, let us recall that there are three quite separate phases in systematics. The first is the *Exploratory Study*, wherein but few specimens are available. It is these few and scattered examples upon which our primary concepts of species are based. Yet these types are often mere scraps or, because of the accidents of exploration, were collected at the margin of a species' range and are

therefore quite likely to be atypical. Specimens accumulate in our museums and the time is eventually ripe for the second phase: an extended survey of the material. This is the *Systematic Study,* resulting in what is often called "the monograph." Here, confronted with considerable diversity and too often with numerous intergradient individuals, the student must determine as best he can the modulus of variability which is to be permitted in his population units; he must delimit his species. Unfortunately, in this chore, the rules of nomenclature are of no help. They only warn the student that every individual must belong to a species, every species to a genus and every genus to a family. There must be no loose ends in this system, for every specimen must be annotated and neatly filed in its pigeon-hole. But since subjective methods only are available in these phases of the work—and these based upon personal concepts—there is no guarantee that any two systematists will agree on group limits. It is for this reason that systematics is sometimes called an art rather than a science. The wonder of it is that there is any agreement.

Fortunately, through the maze of disputation which surrounds much of our work in systematics, a clear path is being opened. It is perhaps the "New Systematics" which some have prophesied. Yet I find in it nothing really new; it is only systematics at work with the tools which lately have been made available to it by other and increasingly more closely allied fields of biological endeavor. Because of its broader scope, this new phase into which systematics is adventuring may be called *Biosystematy,* for it no longer looks upon species as piles of named specimens neatly filed in museum cases, but as populations of living organisms. Any one who has carefully read the recent work on "Genetics and the Origin of Species" by Dobzhansky (1941) can not help but sense the dynamic nature of populations and realize the need to reinterpret our taxonomic units from this standpoint.

There are perhaps some who envision a stabilization of nomenclature in the very near future. I would consider

myself indeed fortunate if I could announce that, ultimately, the biosystematic phase of our science would lead to complete stability. But this privilege is denied me. It is perhaps best that we accept as a principle that our present tools of research will be further perfected and that new ones will yet be discovered. With these will come additional knowledge and, as a consequence, new concepts. If our nomenclature were to be stabilized by fiat—as some have suggested—we would first be required to bring our concepts to a completely static condition. If this were done, systematics would no longer be a science. It would be a filing system capable of being run by clerks, a condition in which it came perilously close to finding itself until revitalized by an application of the pertinent discoveries in other fields of biology in the last quarter century.

Nevertheless, although we can never expect a complete stability of nomenclature in biological systematics (for living populations will continue to erupt new biotypes), something approximating it—a practical stability—can be reached. It is my opinion that this can be achieved through biosystematy. It is in this phase of our work that we can learn the true nature of the population units with which we are dealing and thus define their limits in a more precise manner.

There are perhaps some who would object to the viewpoint that there is need that we have a common concept, that to do so would take away their jealously guarded privilege of personal interpretation, that it would put a stop to their "researches." They are at once both right and wrong. Even a preliminary biosystematic analysis of some group might stop much of their nomenclatural tinkering with it, but it would not stop work on the nature of its species. As a perhaps analogous example from another field, the case of so common a substance as water might be cited.

The early history of the concepts of the composition of this substance will not be rehearsed. But there ulti-

mately came a time when water was understood to be a chemical association of hydrogen and oxygen in certain proportions. From the practical standpoint, the water molecule was chemically defined. But this did not stop research on the nature of water.

It was learned how water molecules could enter into chemical combination with those of other substances (just as the individuals of different species sometimes combine their heredities to produce yet other species). The reactions of water in different environments was studied—its reactions at high and low temperatures and at different pressures, as well as under the influence of other conditions. It was even found to be no simple substance, but to contain a series of isotopes, in part the "heavy water" of our popular literature. But the point is, to the chemist, it is still water—and still composed only of hydrogen and oxygen. In spite of its known solvent powers, no one has yet proposed that, since water and sodium chloride are mutually soluble, water should be chemically redefined so as to include a part of the sodium chloride molecule. It is therefore likely that biosystematy, by defining the genetical limits of the population units we call species, can ultimately bring to our science a nomenclatural stability closely akin to the chemist's concept of the term "water."

However, before this stability can be achieved there must be a greater correlation of our scientific endeavors—there must be a concerted attack on the problem from as many angles as possible, using all the research tools which are available. It is therefore fitting that we briefly discuss the problems of correlative studies.

The Problems of Correlative Studies

There is to be heard on every side a complaint that the various biological disciplines are becoming too highly specialized, that one may be a physiologist, biophysicist, biochemist, anatomist, morphologist, ecologist, mycologist, algologist, pathologist, bacteriologist, systematist,

geneticist, cytologist or any one of other innumerable "ists," but no longer a botanist or zoologist—and certainly never a biologist. Yet those who raise their voices in lamentation might remember that there was a time when to be a biologist was also to be what we call a taxonomist (or more recently a systematist) for that was the only kind which then existed.

In viewing the fields which with bewildering multiplicity have grown up under the general heading of biology, there may be those who sigh for some one to see the Burning Bush—a Moses who will lead us through the wilderness and into a promised land. Yet I have sometimes wondered whether this so-called specialization is as real as some would lead us to believe.

The physiologist, if he is to keep abreast of his science must, among various other things, also be a chemist and physicist. In like manner, the ecologist must not only be well grounded in physiology, but must also be a biogeographer (which also entails a knowledge of geo-history) and, if a plant ecologist, he must know something of the intricacies of soil science—he must also be a pedologist. And it is quite likely that the developmental morphologist is to-day equally trained in anatomy, cytology and physiology, as well as their necessary ramifications which partake of yet other fields. In considering the growth of biology as an organized science developing out of systematics I can not take the view that any of its recognized segments are overly specialized, for they consist of an interlocked system of disciplines, each with its own techniques and methods of approach. If there is specialization to-day it is that imposed by the limits of the individual's ability to encompass or make use of only a portion of man's accumulated knowledge during his normal life-span. No segment of biology—or, for that matter, any science—can exist as an entity apart from others. Yet, throughout the later development of biology, systematics remained apart (or thought it did), for there were

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THE PROBLEMS OF CORRELATIVE STUDIES

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many who held that "the taxonomist needs only to know taxonomy."[2]

There is, however, a constantly increasing group of workers not completely satisfied with the orthodox techniques of systematics. It is this group of workers which is giving impetus to biosystematy. But the student of this broader phase of our science, to do effective work, needs to be conversant with more than the current issue of the International Rules of Nomenclature. It will not be required here to outline in great detail the necessary training of a biosystematist. Briefly, in addition to a familiarity with the usual techniques of the systematist, he should have basic training in such disciplines as morphology, comparative anatomy, cytology, genetics, physiology, ecology, biogeography, physiography and historical geology. And by "basic training" I do not mean introductory or "survey" courses; I mean training sufficiently advanced that he can not only read and interpret the general and technical writings of these fields but also apply their findings to the solution of his own problems.

The time is approaching when the systematist will no longer be completely free to sit before a pile of museum specimens and whittle out species as he may choose, confident that his results will be accepted as authoritative. It will be necessary that they have physiological and ecological soundness, that they fit into their physiographical niche, and that they do not fundamentally conflict with functional biogeography. Also, the historical geologist has every right to inquire into the soundness of the systematist's interpretation of the distribution and phylogeny of a group, for phylogeny, distribution and time are closely linked. Also, the cytologist, peering down the barrel of his microscope, can often see things which confound the careless systematist, while at the same time the geneticist can be more than embarrassing with his ques-

[2] It is true, the taxonomist (or systematist) did make use of morphology, but only such of its findings as would fit into his tidy filing system. Even to-day, every systematist must deal with forms which are morphologically "anomalous" in the group where they are placed.

tions. And since morphology and comparative anatomy both deal with the structure of organisms, the queries of specialists in these fields must be given consideration. Since they all are users of the names of organisms they have every right to expect that these names not only be attached to population units which are biologically sound, but that these names represent concepts of units which are both useful and usable.

He would be a paragon of perfection who would be a well-trained systematist and an expert in all these other sciences at the same time. That is perhaps too much to ask. Yet, if he is to be effective, the systematist must be able to look at his work with something of the perspective of workers in all these fields combined. Furthermore, it is the systematist's privilege also to ask that the workers in these other sciences understand something of his problems: that they also have some training in practical systematics. Greater cooperation between the various fields of scientific endeavor—based on an understanding of the techniques of each—would certainly yield results that would be mutually helpful.

The ways in which the various branches of science can cooperate are innumerable and it would be folly for me to attempt to list them here, even those which have a direct bearing on systematics. However, as a point of departure for possible future discussions, some of the ways will be briefly considered in which systematics, especially of plants, may be more closely linked with other branches of science, and to their mutual benefit.

Historical Geology and Paleogeography: There would seem to be a great gulf lying between the activities of the systematist attempting to apply names to the present floras and faunas of the world and those of the geologist whose concern is an understanding of past continental forms, as well as the construction of an adequately correlated time-scale which reaches back untold millions of years. Yet these fields are not so remote as we might suppose, for wherever possible the geologist relies on the

remains of fossilized organisms for his correlations. The paleontologist, therefore, is a systematist of the past. Unfortunately, too many paleontologists are orthodox geologists with little or no biological training. They see nothing inconsistent in describing what certainly were tropical, or at least subtropical forests lying above the Arctic Circle. If asked how this could be, how such plants could exist under conditions of extreme cold or long periods of darkness they have replied that "plants were different then" or else have invented such interesting hypotheses as a "wandering pole."[3]

In spite of its acknowledged plasticity and diversity, there is a common pattern to life which dare not be ignored, even by the geologist. If his concepts are not consonant with fundamental biology, then it is possible that he should seek some other explanation than that to which he so precariously clings. By being unwilling to view his problems from the standpoint of fundamental biology, he has closed the door to cooperation with the biosystematist.

In dealing with species the systematist is often plagued with the problem of disjunct distributions. Here is one place where the systematist and historical geologist certainly have a common meeting ground. Confronted with the situation of markedly disjunct distributions of living forms, systematists often sit under their favorite vine or fig and whistle up hypothetical vectors such as wind, water or birds to explain the facts for them. I would not say that these agents have not been active. To do so would be biologically unsound. I would only suggest that distributional disjunction *could* be an indication of former land connection and that a serious review of the problem from this standpoint might yield information pertinent to the solution of the problems of both the systematist and paleogeographer. It is my firm conviction that a time will come when the geologist will look as much to the

[3] Chaney (1940) has pointed out that the wandering pole hypothesis leads to no valid explanation, but only to greater difficulties than before.

modern distribution of floras and faunas for information in the reconstruction of paleogeographic areas and the history of the past (especially that of the Tertiary) as he does to the fossils in the rocks.[4] It is encouraging to note that paleobotanists dealing with the Tertiary are making increased use of the herbarium, seeking for cognate forms among the living species.

Ecology: The field ecologist, dealing as he does with mass populations, may note that what have been called species in current manuals may not react similarly throughout their distributions. Such situations may cause serious difficulty in his interpretations. Rather than discuss the problem at length, I will briefly outline one example.

The problem of the beech (*Fagus*) of eastern North America is well known to ecologists. In a systematic study now in progress this population has been found to be composed of several basic, genetic archetypes, each with fundamentally different ecological requirements. The ecologist, therefore, has not been dealing with a single genetic type which reacted differently in various environments, as he had supposed, but with the reactions of different genetic types resulting in organisms which are differentially selected by the environment. The problem of the ecology of the "American beech," therefore, is also a problem in its systematics. This is only an isolated example of the many which might be cited. The

[4] For example, Schuchert (1935) attempted to make use of the distribution of modern organisms in his study of the Caribbean-Antillean region. It is to be regretted that no adequate analysis of the vegetable life of the region was available to him or would be even to-day. Excluding the ubiquitous pan-Caribbean strand-forms, the uplands within and immediately surrounding the area contain no less than ten thousand species of important "index plants" whose distributions are as yet but poorly known. Some areas, as the important Santa Marta massif lying on its southern border in Colombia, an area rising from tropical jungles to permanently snow-capped peaks—and which probably has been emergent since before the Cretaceous—are as yet botanically almost unexplored. An outline of the problems of trans-Caribbean migration may be found in a recent study by Camp (1941). In a brief but interesting paper Dickerson (1941) made pertinent use of biotic evidence in his study of Pleistocene Malaysian land-forms.

corollary to this is that the ecologist can report the findings of his studies in a precise manner only to the extent that the names he uses are critically applied.

Biochemistry and Physiology: I would first wish to emphasize that there is a response-plasticity within the individual, but it is becoming increasingly apparent that the morphological and physiological diversity within a species—its intraspecific variability—may not so much be the result of responses of its individuals in different environments as the expression of slightly different genetic systems. The basis of genetics lies in the fact that morphological characters are genetically controlled. It would therefore follow that the real genetical control is to be found in the regulation of the physiological reactions which are basic to morphological expression. And since physiological reactions result in the production of various compounds, a biochemical and physiological study of a group of organisms may yield corroborative material quite as valuable to the systematist as a study in morphology.

There has been some consideration of the correlation between biochemical reactions and systematics. In general, however, they have dealt with the broader aspects of phylogeny rather than with the delimitation of species. In a recent paper, Krukoff (1939) remarked: "chemical data seldom have received taxonomic consideration in the past, probably because in many cases, chemical work was done on unauthentic materials." He also notes that "The paralysis potency values and certain other chemical data for seeds of various species [of the alkaloid bearing *Erythrina*] . . . would seem to indicate that the soil and climatological conditions are of much less importance than the inherent characters of the plants. The complex and [morphologically] variable species, as a rule, show considerable variations in chemical values, unlike those species that are uniform in their botanical characters and have a limited [geographic] range." He adds: "I think that eventually chemistry will . . . be of more and more

importance to the taxonomic consideration of plants." It is obvious that, for the present, such activities will center primarily around groups of economic importance, but other problems involving organisms of no immediately apparent economic value may also yet be solved by such correlated researches. An understanding of the fundamental biology of a group and the refinements of its nomenclature can go hand in hand.[5]

Morphology and Comparative Anatomy: By the very nature of his techniques the systematist is something of a morphologist, for the basis of his methodology lies in a comparison of differences in structure. Yet there are many structures hidden beneath the surface of an organism's epidermis which the systematist of plants has long ignored. However, there is a growing body of information that such characters are of immediate concern to the worker interested primarily in the delimitation of genera and species. This, the zoological systematist learned long ago.

Botanists of all persuasions have been prone to think that the herbarium is only a storehouse for records of distribution. It is therefore encouraging to note the growing tendency of morphologists and comparative anatomists to visit the herbarium in order to obtain material for study. It is admitted that such material is not always in the best condition. Nevertheless, for certain types of work it is adequate and serves at least to fill in the gaps where better preserved material is not available. At the same time the systematist may realize that the group is in need of careful revision and welcomes any assistance in clarifying phyletic lines.

[5] That such studies should sometimes be carried out on a broad front is indicated by the questions of specific limits in certain populations of *Pyrola*, where some, which are aphyllous and without chlorophyll, have long been considered to be different species from those which have chlorophyll-bearing leaves. Since both types are associated with mycorrhizal fungi and intergrades are known to occur, the problem is no simple one for the systematist. In a recent discussion of the situation in this genus and its problems (Camp, 1940) it was stated that "the ultimate solution . . . does not lie in herbarium study but, rather . . . with aid from the geneticist, the physiologist, and mycologist."

However, in all too many instances, when the systematist seeks to correlate his revisions with the work of the anatomist and morphologist, to his dismay he finds that these workers have failed to give adequate citation of the material upon which it is based. As a further extension of this principle, anatomists and morphologists should acquire the habit of collecting authenticating herbarium specimens at the same time that they collect their preserved material—and from the same organism. All such specimens should be given adequate citation in the literature along with the morphological discussion. For the anatomist to say that two species—closely related in former taxonomic treatments—have quite different vascular systems is meaningless to the systematist unless backed by authenticating specimens; the systematist is too aware of the pitfall of misidentification.

Again, I emphasize the necessity of workers in one field knowing something of the problems and techniques of those in other and increasingly more closely related fields. If the morphologist and comparative anatomist complain that systematists do not pay sufficient attention to their work, the fault may not lie in the nature or quality of these researches, but only in the manner of their presentation. It may be necessary for the systematist to ignore such work (much as he regrets to do so) because there is no way in which it can be correlated with his own researches by means of authenticating specimens deposited in a herbarium and correctly cited in the literature so that he knows where this material may be found.

Cytology and Genetics: These disciplines probably should be treated under separate headings, but they are so closely linked that for our purposes they perhaps can better be discussed together. As Anderson (1937) has pointed out: "Cytology is unique . . . in that it may indicate not only a difference between species or groups of species but may also demonstrate the way in which these differences came about. It is evidence as to the architecture of the very germplasm itself and is, there-

fore, of more fundamental importance than the mere architecture erected by the germplasm. Cytological evidence, therefore, can do more than discriminate between species; it can illuminate species."

When the systematist is confronted with a complex situation it is often imperative that the work of the cytologist be put to practical test by means of the controlled breeding methods of the geneticist, for, on a somewhat smaller scale, he can often reproduce the complexities of a wild population. At times there may be but little in the findings of the cytologist to tell which segments of a population are intersterile or intefertile, whereas this is one of the first things that the geneticist learns. Conversely, the geneticist can rarely tell us how species came into being, while this is perhaps the special province of the cytologist, since he is a student of the architecture of germplasms.

For the systematist, cytology is an excellent tool, for, as Anderson also said, the cytologist "after a few routine examinations, will be able to estimate for the systematist, in advance of the morphological information, the probable evolutionary pattern of the genus or family he is about to monograph." And the geneticist can corroborate or disprove his preliminary hypotheses concerning any unusually complex segments of the group as are also found to be present. Cytology, systematics and genetics—they are an ideal combination when properly correlated, as witnessed by the excellent results of the correlated studies of Babcock and Stebbins (1938) on *Crepis* and those of Clausen, Keck and Hiesey (1940) on a wide variety of genera and species.

The practical aspects of controlled breeding as practiced by the geneticist is at once apparent to the systematist, and there would seem to be no need on my part to elaborate on the extended discussion by Anderson (*loc. cit.*) on the relation of cytology to systematics. Therefore, I will pass by these points and proceed to several items of less interest, but nevertheless of considerable importance to our topic.

In the development of cytology much stress has been laid on the number of chromosomes found in the individual cell of an organism. I would not minimize the importance of these findings, but the systematist, adventuring for the first time into biosystematy, should not be led astray by mere numbers. They must have cytogenetical interpretation and be derived from a sufficiently large sample of the population before they become significant. To say that a species is characterized by a certain number of chromosomes and this based on the examination of a single individual, or even the individuals of any particular region, may lead to serious errors. Anderson's work on *Tradescantia* (as reported in his 1937 paper cited here, and in others) is proof of the regional nature of cytological variants; for much more complex situations, the papers by Wahl (1940) on *Carex,* and Winge (1940) on *Erophila* (*Draba*) may be consulted.

Yet there is a value, even to the studies of individual organisms, if they are done in such manner that they become common scientific property. It may appear that I am scolding, but this is not my intention. The minor tragedy of so many of these reports is that, from the practical standpoint, they are of no use to the systematist, for they are not backed by authenticating herbarium specimens.[6]

[6] It is true that many chromosome counts are made on root tips, and these often from sprouting seeds which would not be easily identifiable. There are two ways out of the situation. A set of plants could be raised from the same lot of seed; or, better yet, the plant which bore the seed (or at least a suitable portion of it) could have been sacrificed as authenticative material to be cited as has been mentioned in the foregoing paragraphs under the heading of "Morphology and Comparative Anatomy." Where parts other than sprouting seeds are used there is generally ample opportunity to obtain adequate specimens from the same individual, thus insuring against the loss of a single authenticate. Wahl (*loc. cit.*) in his cytological studies of *Carex,* has adopted a method which is to be commended. Three sets of adequate specimens were made from the various individuals studied, two of these being placed on deposit in separate herbaria, and the third designated as the "traveling set" to be loaned to any one similarly interested in this complex genus.

In going through the more recent cytological literature, it is encouraging to find an increasing number of students who realize that our current concepts of specific limits are not necessarily valid, that the names we use to-day may not be those we will use in the future, and that a report based on a few individuals may not represent the condition throughout the entire distribution of a species. It is probable that each worker could devise some suitable way in which to authenticate his findings and thus give reasonable assurance of the permanence of the record and also that the material is available to systematists, who will certainly use it in future studies of the group. It is suggested, in addition to the usual data which would appear on the label, that the chromosome count also be appended, as well as a citation of the place of publication containing discussion of the data. In such manner the work of the cytologist, with but little additional effort, is brought into close correlation with that of the systematist. Likewise, the geneticist should also learn that the herbarium is a place where he can store his validating records. And if the specimens are adequate, the systematist will find them of considerable help in his work.

Systematics with Limited Facilities

In viewing the broadening scope of systematics, it is likely that many workers, particularly those in the smaller institutions, may feel that the lack of facilities will seriously hamper their studies. Nevertheless, it is my firm belief that it is just this body of workers, in the aggregate, who will yet make the greatest contribution to the science of systematics. This may be briefly discussed under two headings: biosystematy and mass collections.

Biosystematy: There is no need, even in this expanded phase of our science, for elaborate paraphernalia. An ordinary microscope of good resolving power, a few simple stains, a bit of garden or a small corner of a greenhouse will suffice. Nor is it necessary that we gather material from the farthest corners of the world. The

species at our doorsteps for a long time will yield information as startling and important as those from far-off places. Here is one of the new biological frontiers.

Also, from the academic point of view, an active project in biosystematy under the supervision of even a single instructor would yield so many and such varied problems of immediate and practical importance that it would be a veritable fountain of subsidiary topics which could be parceled out to a series of students working for their higher degrees. Thus, although each student would be primarily specialized in his techniques, he would, by contact with the other phases of the problem, receive a more rounded background in his general training than he might otherwise achieve.

Mass Collections: It is also probable that there may be some workers who do not have available even the small plot of ground necessary for the growing of living plants, or who have no great inclination toward the cytogenetic analyses necessary in biosystematy. They may still feel that work with herbarium specimens is the ultimate in systematics. Yet such a worker may complain that he does not have on file a sufficiently representative number of species of a group to do effective work. To-day, this is no longer an excuse for shirking active systematic research of a most significant type. No herbarium, no matter what its size, can give us the real information we need. It can be gained only by going out into the field and returning with sufficient material, carefully collected, and with adequate data. The herbarium is only the laboratory where the final stages of the research are conducted and where the material used is stored for future reference. It is in these extended studies of large populations—validated by mass collections—where the systematist lays the real groundwork for a study of species.

For example, it may be known that a species has both pubescent and glabrous phases which, in a particular area, may appear together. Since they seem to "intergrade" the systematist may think that the differentiation

of such "forms" is of little importance and that "they are likely to be met with throughout the range of the species." A careful census of a statistically sufficient number of individuals in various areas may indicate that there are no "intergrades" but, rather, that there are different *proportions* of these individuals in different areas. In this manner the student is taking the first and necessary step in the genetic analysis of a species. As Krukoff (*loc. cit.*) pointed out, in *Erythrina,* where important medicinal compounds are sometimes present, minor differences in morphology may be an indication of the presence of exceedingly different biochemical constituents. The extension of this principle is certainly true in the majority of species and reaches practical application in horticulturally and economically important groups. This is the functional phase of systematics. Those who have had anything to do with the selection of material from the wild for breeding-stock in horticultural work know how important apparently minor characters may be as "indicators" of more important items.

There is no opportunity in this place adequately to discuss the value of mass collecting as applied to an analysis of species, or the ways in which it may be carried out. However, for those who are interested, I will refer only to the recent work of Fassett (1941) on the *Rubus odoratus* and *R. parviflorus* complexes. There are those who would seek to solve the problems of this troublesome genus by the description of hosts of utterly useless "new species." By so doing they are bringing us no closer to an understanding of the group; they are only further confounding us. Professor Fassett may lament the fact that his material can not be filed so neatly in an orthodox manner in museum pigeon-holes as the curators of some herbaria might wish. But his species do represent living and dynamic populations. It is this kind of interpretation which we systematists must put on species if our work is to be effective and truly significant.

To many the sole function of the herbarium is that of a place where records of distribution are kept. The collecting of new county or state records, or the local appearance of newly adventive weeds, or their spread, is certainly to be commended, for it is a valuable addition to our knowledge. But such activities can not lead us to an understanding of species. The systematist who neither is concerned with nor makes an attempt to study and understand the nature of the internal variability within species and species-groups is, to-day, scarcely worthy of the name. He has closed his consciousness to a century of research directed toward an understanding of the origin and cause of the diversity of living organisms; he is still traveling under the banner of those who believe in the perpetual fixity of germplasms. His counterpart is to be found in the collector of postage stamps who knows neither geography nor history—and who does not want to learn.

The systematist, being constantly berated by his confrères in other fields (who demand from him peculiarly static concepts which they would not tolerate in their own studies), has attempted to maintain an archaic *status quo*—even by the use of rules. And here, perhaps unknowingly, he has also failed. It would therefore seem only logical that systematists venture forth more often among populations of living organisms, complex and confusing as they sometimes are. With our present knowledge of the causes of this variability, elementary as it certainly is, we may find these populations nomenclaturally less troublesome than we had supposed.

CONCLUSION

We are now standing on the threshold of a new era in the science of systematics. The day of the taxonomist who putters alone in his herbarium with an other-worldly stare is done. He must shed his robe of academic classicism and seclusion, brush off the accumulated dust of the centuries, and come face to face with the dynamics of

living populations. To-day, as never before, workers in all fields of pure and applied science are beating a path to the herbarium door, seeking for help in the solution of their own problems. There must be no shirking of our responsibilities. We must no longer be mere filers of dead specimens; we must be namers of living organisms. And we must have as an ideal that these names should be applicable not only to population units which are biologically sound, but also that they be of such a nature that they are both usable and useful to all those who have need to know the names of organisms.

It is therefore fitting on this occasion that we dedicate a herbarium to the continued memory of one who was a collector of specimens. (And he was a good one. I know, for I have studied many of his gatherings from northern climes as well as from steamy tropic jungles.) But he is much more than a collector and namer of dried specimens. He is also known for his firm grasp of many of the fundamental problems of biology and his numerous contributions to their better understanding. I am certain, if the choice were his, that this herbarium—built mostly through his own toil—would not be dedicated to himself, but to a continued study of the nature of living things.

Let this spirit of his be with us—always.

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PARASITISM AND EVOLUTION[1]

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THE term "Parasitism and Evolution" has various connotations for biologists. To some, it refers to the modifications that parasitic organisms have undergone in their descent from free-living ancestors; to others, it means the ways by which parasites may have affected, biochemically or otherwise, the evolution of their hosts. In some cases, it is believed that parasites may even have caused the extinction of the forms attacked. Still other workers are impressed by the remarkable series of adaptations which many parasites have undergone for development in and transfer to various hosts. For example, in the life history of a single parasite, there may be involved as many as four separate hosts; these may live in various habitats and belong to widely separated taxonomic groups.

In this discussion, however, another phase of the problem of parasitism and evolution will be considered. This is one in which it seems to me that speculation has often outdistanced the factual evidence. The result is that a generalization has come to be accepted widely although it is based on only a few examples, while the exceptions, I believe, have been all too commonly glossed over.

I am referring to the view that pathogenicity to the host is really a disadvantage to the parasite and that consequently long-standing parasites, by the processes of evolution, have much less of a harmful effect on the host than have recently acquired ones. According to this conception, it is mainly the latter which are productive of severe or even fatal disease.

This view carried to its extreme has led to statements in recent literature such as "a high degree of pathogenicity of a parasite may be considered *prima facie* evidence

[1] Presidential Address, Western Society of Naturalists, Stanford University, December 30, 1941.

of a recent and still imperfect development of the host-parasite relation." (Chandler, 1940.) Or, "a parasite pathogenic to its host is considered to be relatively new to it." (Fantham, 1936.) Or the supposed corollary of this proposition: "There is a sort of mutual adaptation between the two which is developed in proportion to the time that the relationship of host and parasite has existed." (Chandler, 1940.) Various investigators have come to rely upon the type of parasite-host reaction as indicating, therefore, the length of time a parasite and a host have been associated. If the reaction is severe, resulting in disease or death, then the parasite is relatively new for the host; if the relationship results in no reaction or only a slight one, then so runs the argument, host and parasite have been long associated. (Hegner, 1926.)

Let us examine briefly some of the evidence on which these rather sweeping conclusions are based. Perhaps one can illustrate some of the difficulties which follow from the line of reasoning by referring to the amoebae of man's digestive tract. Conservatively speaking, we may hazard a guess that one out of every five persons in this country harbors a harmless or a commensal amoeba in his intestine and one out of every 20 a harmful or pathogenic species. Should we assume that the mere fact of pathogenicity is an indication that the latter species has been more recently associated with man than have the harmless ones in the same environment? On the other hand, all the commensal and pathogenic species of human amoebae are present in the higher apes, and if man, as seems probable, acquired his infection from them, the degree of pathogenicity is hardly a reliable guide to the length of time man and his intestinal amoebae have been living together.

It is difficult to discover who first formulated this idea of an evolution occurring in the degree of host-parasite relationship, with the result of a gradual loss in pathogenicity. Perhaps Van Beneden (1875, 1885) in his "Animal Parasites and Messmates" of nearly 70 years

ago was one of the first to set forth the view fairly definitely when he wrote: "The Parasite is he whose profession it is to live at the expense of his neighbor, and whose only employment consists in taking advantage of him, but prudently, so as not to endanger his life. He is a pauper who needs help, lest he should die on the public highway, but who practices the precept—not to kill the fowl in order to get the eggs. It is at once seen that he is essentially different from the mess-mate who is simply a companion at the table. The beast of prey kills its victim in order to feed upon his flesh, the parasite does not kill; on the contrary, he profits by all the advantages enjoyed by the host on whom he thrusts his presence." (Beneden, 1885, p. 85.)

There has been a gradual development of this concept since it was first proposed, and such eminent authorities as Woodcock in Lankester's "Treatise on Zoology" (1909), Minchin (1912) and Theobald Smith (1921) did much to popularize it and to apply it to modern concepts of epidemiology. There is indeed strong circumstantial evidence that such adaptations, resulting in decreased pathogenicity with long-continued parasitism have occurred many times in the past and are perhaps still occuring to-day. But that such occurrences are universal, so that we may therefore argue back from the degree of pathogenicity of a parasite to the length of time the parasite has been living in a particular kind of host, is a view which, I maintain, is hardly warranted by the evidence at our disposal.

At the outset there seems to be a contradiction between two supposed evolutionary developments. On the one hand, we have the commonly accepted view of the relation of the parasitic way of life to those types of association which we call commensalism and symbiosis. On the other are these views I have mentioned, of decreased pathogenicity with increased length of parasitism.

Let us examine the dilemma a little more closely. Most parasitologists would agree that free-living forms were

the predecessors of their parasitic relatives and that parasitism in most cases followed upon some commensal or symbiotic relationship. In most instances, those forms which are found in such relationships are more like their free-living relatives than are the true parasites. If this be the case, then parasitism with accompanying pathogenicity is the result of a long rather than of a short period of association, and we are justified in concluding that the pathogenic *Endamoeba histolytica* is really an older inhabitant of man, in terms of evolution, than is the commensal and harmless *Endamoeba coli,* which has not yet learned, evolutionarily speaking, to swallow *in vivo* epithelial cells or blood corpuscles, in preference to the bacteria or the food particles in the gut lumen.

In his paper on "The Evolution of Parasitism among the Protozoa" (Fantham, 1936) the late Professor Fantham postulated a phylogeny of the amoebae of man. He believed that the common fresh-water amoeba, particularly of the *limax* type, came first in the series, then followed a human intestinal amoeba such as *Endolimax nana,* in morphology very much like a free-living limax type, next came *Endamoeba coli,* and finally *Endamoeba histolytica,* which, he said, "has progressed still further along the line of parasitism" (p. 317).

In the same article, however, Professor Fantham concluded: "In parasites long resident in their hosts, a mutual state of harmony or tolerance is set up to a greater or less degree. The newer a parasite is to its host, the less is the harmony that exists between them" (p. 324).

There seem to be two ways out of this dilemma. One is to assume that the non-pathogenic effect of a parasite on its host may occur in two separate periods of the evolution of the former: once, before the parasite has evolved completely from a symbiotic or a commensal state and before it has successfully adapted itself to living at the expense of other organisms; and secondly, after a comparatively long period of parasitism, when mutual adaptations of host and parasite have reduced it to a stage of

comparative harmlessness. Such a thesis can be maintained logically. But in the present stage of our knowledge of the evolutionary past of parasites, there are few parasitologists who would hazard an opinion that parasite *A* is relatively harmless because, from the standpoint of evolution, it is just embarking on its nefarious career and hasn't learned perhaps how to be successful burglar or pickpocket; and that parasite *B* is, on the other hand, relatively harmless, because it is an old hand at the game and has learned that if it doesn't steal too much, the loss will hardly be noticed, while grand larceny or murder may quickly cause the destruction of the malefactor. In any case, one can not maintain that relative harmlessness is *prima facie* evidence for long parasitism, and severe pathogenicity equal evidence for its relative newness.

There is, however, another way out of the difficulty, which, nevertheless, seems to me to be even less satisfactory. Rabaud (1928) and others question the usually accepted line of evolution leading from commensalism or symbiosis to parasitism and maintain that each of these relationships came into existence more or less independently (pp. 76, 43–44). Under certain conditions, a host-parasite relationship results in commensalism; under others, it may result in parasitism. According to this view there is no progressive adaptation leading from one stage to the other; commensalism or symbiosis are not stages ending in parasitism; each relationship has arisen all at once and each represents an end-point in any particular evolutionary development.

Such a theory is so much at variance with what seems to be an overwhelming mass of evidence (Wenrich, 1935) for the development of parasites from free-living ancestors through a series of commensal and symbiotic relationships, that few workers would adopt it without more facts than have been so far marshalled in its favor. Furthermore, just as gradual adaptations, by this theory, have not produced parasites from free-living forms, neither have they resulted in a gradual decrease in patho-

genicity with increased length of parasitism. Just as parasitism would have occurred in one jump, so pathogenicity or its absence would occur just as fortuitously and just as independently of the time element.

There are, or so it seems to me, numerous instances of comparatively new infections which have been established in a host with little or no pathogenicity; just as some long-standing parasitic infections may still produce some very serious symptoms. Much of this evidence is to be found in the field of experimental parasitology and some from the known history of disease caused by animal parasites.

The examples chosen have been drawn mainly but not entirely from the group of the parasitic Protozoa. They should be of interest, however, to all naturalists and not merely to the technical parasitologist.

The intestinal amoebae of man have already been mentioned. Dobell (1931, 1933, 1936) in a series of very painstaking researches has demonstrated that all the major amoebae of man are to be found in monkeys. It is theoretically possible that the various primates have acquired their intestinal protozoa from man rather than *vice versa*. But the very wide-spread occurrence of these parasites in certain kinds of monkeys, together with the findings that apparently every major intestinal protozoan of man—amoebae, flagellates and ciliates—occurs in wild-caught monkeys (Hegner and Chu, 1930, 1930a) leads to the view of the monkey-man rather than to the man-monkey route of parasite acquisition.

If man acquired his intestinal protozoa fully formed from his ancestors, they must be fairly "old parasites" from the standpoint of human evolution. In the monkey, as in man, the amoebae are apparently harmless except for one: *Endamoeba histolytica* (Johnson, 1941; Ratcliffe, 1931; Hegner, Johnson and Stabler, 1932; Eichhorn and Gallagher, 1916), which may be highly pathogenic or even fatal. Are we justified, therefore, in singling out the pathogenicity of this one species of intestinal amoeba as

"*prima facie* evidence" that it is a recently acquired parasite, and in concluding that the harmlessness of the other amoebae of man is in itself an indication of a much longer time that "the relationship of host and parasite has existed"? Such conclusions seem as unjustified for the human amoebae as they are for certain other groups of parasites.

The intestine of man and of other vertebrates harbors not only amoebae but also various species of flagellates. Some of these are highly pathogenic for their hosts; others are apparently entirely harmless. A great many of them may be transferred to and may establish themselves in foreign or what some investigators are inclined to call "abnormal" hosts. Such hosts may be as widely separate as birds and mammals. Here it seems we should find ample evidence for the thesis that high pathogenicity indicates recent parasitism, and low pathogenicity a mutual adaptation resulting from long-standing association.

Two common intestinal flagellates of man and of certain other mammals belong to the genera *Chilomastix* and *Trichomonas*. In most of these hosts, they are non-pathogenic, as a result, shall we say, of long-continued association with their hosts. Young chicks, however, are very easily infected with mammalian species of these flagellates, which carry on their life histories normally in their new hosts. *Chilomastix*, from guinea pigs, as both Hegner (1929, 1929a) and the writer (Ball, 1931, 1932) have shown, will encyst, divide and excyst in the chick cecum; *Trichomonas parva* (Hegner, 1929a, pp. 35–36) of the rat has persisted in fowls for at least 191 days and *T. hominis* from man for at least 141 days (Hegner, 1929).

Here are instances, and only a few are mentioned, for many foreign species of flagellates were found to live normally in young chicks, in which a new parasite is established in a host, but where no pathogenicity results. If such associations should occur in nature, the parasitologist or the evolutionist would indeed be in error in con-

cluding that the non-pathogenicity was the result of a long-standing connection between host and parasite. Again, the effects of the parasite are poor guides for determining the length of association.

But there are other trichomonads that may be highly pathogenic to their hosts. Such a species is *Trichomonas gallinae*. In pigeons, doves and certain other birds, it may produce severe symptoms and even death (Cauthen, 1936; Levine, Boley and Hester, 1941). It is possible to transfer this parasite experimentally to various raptorial birds (Stabler, 1941). Where the infection is successful, disease conditions may develop, resulting in the death of the host; or else the infection may be successfully established, and the birds remain perfectly healthy. Once again, the degree of pathogenicity is the result of various diverse factors and is in no way conditioned by the length of time that host and parasite have been associated.

If we turn our attention to some of the blood-inhabiting protozoa, we find that there are many instances where pathogenicity is unrelated to length of host-parasite relationship. Among the species of bird malaria found in nature, some ten species can be transmitted experimentally to an unfamiliar or, in the terminology of some workers, to an "abnormal" host. (Hewitt, 1940.) Some species are highly pathogenic to the canary, resulting in the death of many birds; while other species produce little or no effect on the experimental host although infection becomes established. If one examines a table (Hewitt, 1940—table 8) of these various species of malaria in a single experimental host, he is struck by the great diversity of behavior. Some parasites of a relatively high pathogenicity develop rapidly, some slowly; some are demonstrable in the blood for a long period of time; some for only a few days. The conclusion to be drawn from a great number of extensive experiments is that all types of variations occur in the behavior of these parasites when they are introduced into foreign hosts.

Some species are highly lethal; some find conditions so unfavorable that they are barely able to get along with very impaired reproductive powers, and others develop in the new host, sometimes more successfully than in the original one from which they were isolated in the wild, without producing any marked untoward effects in their new home.

In addition to the canary, various other birds, both wild and domesticated, have been used in cross-infection experiments with bird malaria. In many instances, these are distinctly "foreign" hosts, such as the chick or the duck, not normally infected in nature with these species (Wolfson, 1936, 1937, 1937a, 1939, 1940; Hegner and West, 1941, 1941a; Hewitt, 1940; Coatney, 1938; Manwell, 1933). Host-specificity seems to be very loose in many of these forms; for example, a species first isolated from a wood thrush has been transmitted to a canary, to a duck and then to a chick (Hegner and West, 1941a). In most of these "new" or "foreign" hosts, the malaria parasite has a very low pathogenicity or is apparently harmless, even though infection may result in extensive invasion of the red cells and completion of the parasite's life cycle with the production of gametocytes. At least one species, on the other hand, was highly pathogenic to ducks (Wolfson, 1940) and moderately so to young chicks (Coggeshall, 1938).

In one series of experiments (Hegner and West, 1941), a strain isolated from the English sparrow killed 60 per cent. of canaries, that is, it exhibited severe pathogenicity in one kind of new host, but the same strain did not produce symptoms in ducks, another new host of a different sort, although infection lasted in some cases at least two weeks and gametocytes developed. In one new host, infection produced severe disease; in another new host, infection was practically harmless; other factors, and not the newness of the host, determined the pathogenicity of the relationship.

With respect to human malaria, certain statements have found their way into the literature which should also, it seems to me, be re-examined in the light of fuller evidence. It has been maintained that native races living in endemic areas show an inborn resistance to malaria. For example, as the result of many generations of adaptation, the Negro is supposed to exhibit less severe symptoms than does the white man, because of longer association between host and parasite (Culbertson, 1941; Faust, 1931).

More recent evidence, however, has shown that this so-called "racial" immunity to malaria is rather the result of "premunition"—a tolerance established as the result of a latent infection occurring early in life (Smith, 1934, p. 69; Burnet, 1940, pp. 284, 285; Sergent, 1935). As Schüffner, Swellengrebel *et al.* (1932) have shown among the natives of Malaya, the tolerance exhibited towards malaria is acquired at the cost of high morbidity and mortality among the children. Even among the Negroes of our Southern States whose refractoriness to induced malaria is well known (Boyd and Stratman-Thomas, 1933) and is possibly to be explained as an acquired rather than a racial immunity, the death rate from malaria is much higher than among white persons in the same area (Brown, 1940). Although this difference in mortality rate may be due in part to inadequate treatment in the Negro, these figures show that even in the adult, malaria is by no means the relatively harmless disease in the Negro that certain writers have implied to be the case.

Furthermore, among those investigators who maintained that malaria resistance was innate in the Negro, it was recognized that these differences were not the same for all species of malaria. Even though the white race was believed to be more susceptible than the black to tertian malaria, there was evidence that no such racial difference existed for quartan (Culbertson, 1941; Boyd, 1934).

One other example from the malaria parasites indicates the unreliability of following the degree of pathogenicity as a clue to length of time host and parasite have been associated. One species of monkey, *Silenus* (*Macacus*) *irus*, has been found infected in nature with three species of malaria, which produce slight or no symptoms (Hegner, Root, Augustine and Huff, 1938; Sinton, 1934) in this host. One of these species of malaria usually is fatal if transferred to a foreign host—another kind of monkey, *Silenus* (*Macacus*) *rhesus;* the other species transferred to the same host causes only a mild infection (Knowles and Das Gupta, 1932). To complicate the picture still further, the former species can be transferred to man, another foreign host, in whom it usually sets up a mild infection; with the Negro apparently less susceptible than are white persons (Milam and Coggeshall, 1938).

If we consider briefly some of the other blood or tissue-inhabiting Protozoa, we find similar host-parasite relationships. Among the severe infections produced by parasitic Protozoa in man are those caused by the members of the genus *Leishmania.* Two diseases they produce are kala-azar, with a death-rate in untreated cases of probably at least 75 per cent.; and espundia, found in parts of Central and South America, where the symptoms frequently are extensive destruction of the mucous membranes of mouth, nose and throat, with death a not unequal sequel.

Nevertheless, what evidence we possess indicates that "Leishmaniasis," in the words of Adler, a leading investigator (Adler, 1940), "must be regarded as one of the oldest of human diseases." Espundia, in his opinion, was certainly present in the New World before Columbus, since the disease was pictured unmistakably on Inca drinking vessels (Moodie, 1923); and there is good evidence both from the standpoint of epidemiology and from the differences in their intermediate hosts that kala-azar in South America is at least as old and is not a recent importation. If we accept Adler's view of the antiquity

of *Leishmania* infections in man, we have another instance of the failure of a long-standing infection to identify itself as such to the parasitologist through low pathogenicity and comparatively slight interference with the normal activities of the host. If one should object that the time interval in this instance is too short for evolution to have produced any noticeable effect, it may be pointed out that the period of time is of the same magnitude as that which is supposed to have produced immunity in different races of man to trypanosomiasis, malaria or hookworm.

It is from among the trypanosomes that examples are most frequently cited of recent parasitism being accompanied by high pathogenicity and of long association indicated by comparative harmlessness (Caullery, 1922; Woodcock, 1909; Burnet, 1940; Hegner, 1926; Minchin, 1912; Smith, 1934; Hyman, 1940, p. 111; Fantham, 1936; Taliaferro, 1929). The trypanosomes of the wild game of Africa are comparatively harmless, yet some of them (*T. gambiense* and *T. brucei*) may be highly pathogenic when transferred to foreign hosts, such as man or his domestic animals. In fact, some investigators believe that one of the most virulent trypanosomes of man, *T. rhodesiense*, first discovered in 1909, probably came into existence about that time either as a new species or as a race of *T. brucei* capable of infecting man.

No one would be justified in denying that adaptations of this sort have occurred in the history of host-parasite relationships, and evidence for their occurrence is probably strongest in the *Trypanosomidae*. The thesis that is being questioned is rather the validity of assuming that this is a universal phenomenon, so that one can postulate the length of the relationship merely by the degree of pathogenicity.

Even among the trypanosomes, recent observations cast a certain shadow of doubt on these interpretations. Recent investigations indicate that although the wild game of Africa can be infected experimentally with *T.*

gambiense, it is very probable that this parasite does not occur in nature in any wild game animal (Chandler, 1940; Craig and Faust, 1940; Duke, 1936, 1937, 1937a); consequently, we are hardly in a position to determine the "natural host" of this particular parasite. It may have arisen as suddenly as did apparently *T. rhodesiense*. On the other hand, the domestic animals introduced by man, such as sheep, cattle, goats and pigs, have been found to harbor the parasite and to serve as true animal reservoirs without displaying symptoms (Craig and Faust, 1940; van Hoof, Henrard and Peel, 1937, 1937a). Both man and the domestic animals accompanying him may perhaps be considered "foreign" hosts of *T. gambiense*. The intimate nature of their relationship must have carried the infection from one type of host to the other in a very short space of time. Nevertheless, of two possibly "new" hosts for a single kind of parasite—both infected for about the same length of time—one exhibits severe symptoms and one practically none, yet in both the parasite has established itself and become infective for the intermediate host. Lack of pathogenicity in domestic animals is not due to inability of the parasite to complete its life history.

Comparing the situation in *T. gambiense* with that in *T. rhodesiense*, it appears that it is hardly valid to generalize from what seems to have happened with the latter parasite in the face of what seems to have occurred with the former. *T. gambiense* is pathogenic for one supposedly new host, man; harmless in others, certain domestic animals; *T. rhodesiense*, or the closely related *T. brucei*, is pathogenic to both man and domestic animals. That the latter is necessarily pathogenic because it is a new parasite or a new parasite because it is pathogenic (Fantham, 1936), are not conclusions warranted, I believe, when other species of trypanosomes are considered.

In another trypanosome of man, *T. cruzi*, the widespread occurrence of the infection in native mammals in endemic areas and the infection of the intermediate host

in the absence of demonstrable human infection have led most workers to consider lower animals as the natural hosts of the parasite (Galli-Valerio, 1920; Chandler, 1940; Culbertson, 1941). If man is a relatively new or a foreign host for the trypanosome, he exhibits a low rather than a high susceptibility, for he is infected with difficulty, and probably the majority of infected humans show few or no symptoms.

These are only a few out of a large number of examples of protozoan parasitism, examples which, I believe, fail to substantiate the doctrine that severe pathogenicity is the mark of a new parasite and relative innocuousness the sign of a long-established one. There are those instances where the death of the host may occur as the result of the infection but subsequent to the completion of the parasite's life history. The ciliate, *Ichthyophthirius*, an ectoparasite of fish, furnishes an example. Here the death of the host is a matter of indifference as far as the parasite is concerned. Furthermore, there are to be considered those relationships where the death and decay of the host is actually an aid to the dissemination of the parasite, as in some of the tissue-dwelling Myxosporidia which produce considerable tissue destruction and often death of the fish host (Kudo, 1934). In these and in other cases of parasitism in nature, long association of host and parasite has not resulted in a relatively harmless relationship.

Evidence of a similar sort can also be found among the Metazoan parasites. Among the more severe worm infections of man are those caused by the blood flukes belonging to the genus *Schistosoma*. In some endemic areas, they cause "more sickness and death than any other parasitic disease" (Chandler, 1940); a death rate of 10–20 per cent. is not at all uncommon among untreated cases, with severe and disabling symptoms among many who do not succumb. In some areas, the infection may involve 60–85 per cent. of the population. Here is a parasite which is highly pathogenic for man, yet it is one of the oldest human parasites of which we have any record. Not

only are the symptoms described unmistakably in the papyri of ancient Egypt, but the ova of one species, *S. haematobium*, have been discovered in the bodies of mummies of 1250 B.C. (Moodie, 1923), and there is evidence that the oriental form *S. japonicum* is probably as old (Hegner, Root, Augustine and Huff, 1938). One would not be justified, therefore, in assuming that the severity of *Schistosomiasis* indicates a fairly recent human disease, since we have actual evidence that it is a very ancient one.

The results of experimental work with various helminths indicate that many factors beyond mere length of association play an important part in the incidence and pathogenicity of worm infections in new hosts. Investigators working with hookworms, or *Ascaris*, or tapeworms have shown again and again the important roles played by age, genetic constitution, vitamin deficiency, previous type of host, etc., in establishing infection and in the effects produced on foreign hosts. Rarely does a helminth introduced experimentally into a foreign host run riot and produce severe symptoms. On the contrary, the new host at first is apt to be much more resistant or to exhibit very little effect (Kotlán, 1934; Cameron, 1934; Culbertson, 1941; Scott, 1928). One might cite the great difficulty in producing cross infection between man and pig with their respective strains or species of *Ascaris* (Hiraishi, 1928; de Boer, 1935; Clapham, 1934), or the behavior of cat and dog strains of the dog hookworm *Ancylostoma caninum*.

In this species, it has been shown that a strain isolated from the dog is much more infective to other dogs than it is to cats, and that the cat strain infects other cats much more easily than it does dogs. Moreover, in the cat strain, the infectivity can be reversed after one passage through the dog so that it now infects dogs very readily and cats hardly at all. However, after several generations in cats, it apparently regains its infectivity for its original host (Foster and Cort, 1937). The dog strain is apparently more stable and does not show this reversibil-

ity (Scott, 1930a). It is believed to represent perhaps the ancestral strain (Scott, 1930).

The important point for this discussion is that in a single species of parasitic worm, infection may take place in a "foreign" host with no marked change in pathogenicity. In fact, if we accept the view that the dog is the original host (Foster and Cort, 1937; Scott, 1930), then in the more recent host, the cat, infectivity, size, growth-rate and egg production is lowered rather than increased. May we say that here we have a case similar to the change believed to have occurred when *Trypanosoma rhodesiense* arose from the closely related *T. brucei*? In the hookworm, however, the race in the new host was less disturbing than in the old; in the trypanosomes, the reverse was the case. Surely any generalization must take into account either possibility.

Similar observations have been reported for the gapeworm of birds, *Syngamus trachea* (Taylor, 1928), in which a strain derived from the starling was less infectious and resulted in a lower death rate for chickens than did a strain derived from other chickens.

In *Trichinella spiralis,* the organism causing trichinosis, Oliver-Gonzalez (1941) found that the virulence of the parasite was decreased by successive passages through rabbits or guinea pigs, but that its virulence was increased by successive passages through rats.

In this survey of instances where degree of pathogenicity would be but a poor guide for determining the length of time host and parasite have been associated, I have neglected almost entirely those cases offering contrary evidence. But what I have been endeavoring to point out is not that such mutual adaptations between host and parasite may not have occurred. It is rather that generalizations have been drawn from certain examples and contrary evidence has been overlooked. In the face of the kind of examples referred to in this discussion, there seems to me to be grave doubt for acceptance of the statement that "a high degree of pathogenicity of a

parasite is *prima facie* evidence of a recent and still imperfect development of the host-parasite relation." Evolution may, in many cases, have brought about a mutual adaptation between host and parasite resulting in relative harmlessness of the relation, but in other instances no such decrease in pathogenicity seems to have occurred; and in still others as the parasite becomes better adapted for life in its host, it has become rather more than less capable of producing disease.

Perhaps, as biologists, we may all agree on one aspect of nature, namely, its exceeding variety. Even a parasite may choose the course of manifest destiny and find aggressiveness more attractive and more valuable than an existence of peace and symbiosis.

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REVIEWS AND COMMENTS

EDITED BY CARL L. HUBBS

In this section reviews and notices are given of current publications on general biology and of specialized works which have an important bearing in this general field. Emphasis is given to books and major articles which fall within the special scope of The American Naturalist, in that they deal with the factors of organic evolution.

Reviews and Comments are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, University of Michigan, Ann Arbor, Michigan. All opinions are those of the reviewer.

Evolution The Modern Synthesis. By Julian Huxley. New York: Harper and Bros., 1943: 1–645. $5.00.

It would probably be no exaggeration to call this the outstanding evolutionary treatise of the decade, perhaps of the century. The approach is thoroughly scientific; the command of basic information amazing; the synthesis of disciplines masterly. It is meant for advanced students and particularly for biologists. All biologists will profit by reading the book, and many professional workers sorely need to learn the lessons which it presents so clearly and penetratingly. The dedication "to T. H. Morgan: many-sided leader in biology's advance" will be especially appreciated by American zoologists.

Since Julian Huxley is so well able to speak for himself, and has the habit of epigrammatic summarizations, I present his views in his own sentences, selected and rearranged for this purpose, and occasionally slightly altered in a verbal way. Here are some of his more general ideas on evolution:

Evolution may lay claim to be considered the most central and most important of the problems of biology. Darwinism to-day still contains an element of deduction, and is none the worse for that as a scientific study. Evolution must be dealt with under several rather distinct heads: origin of biologically discontinuous groups; origin of adaptations; extinction; origin and maintenance of long-range evolutionary trends. Comparative Evolution is destined to become as important a branch of biology as Comparative Anatomy.

A large number (possibly the majority) of genes exert their effects through the intermediation of a process operating at a definite rate. Studies on relative growth sometimes lay bare the genetic mechanisms underlying

evolution. Geographical divergence is a general evolutionary phenomenon. Evolutionary change is not completely at random. It is an advantage to an organism to have its normal constitution as harmonious as possible.

Adaptation is strongly championed as a factor almost universally of major and indispensable significance in evolution. I have gathered together some of Huxley's key thoughts on this subject:

The Lamarckian interpretation is neither necessary nor tenable. Modern biology repudiates lamarckism. Evolution is a joint product of mutation, recombination and selection.

Adaptation is omnipresent. It has been all-important in evolutionary progress. Every organism cannot be other than a bundle of adaptations. Many of the apparently useless features used in diagnosing species are correlated characters.

Organisms are selected, not on the basis of a conformity to an ideal plan, not in relation to complete functional efficiency, but on the basis of survival. To produce adapted types by chance recombination in the absence of selection would require a total assemblage of organisms that would more than fill the universe, and overrun astronomical time.

Selection-pressure forces life to occupy every geographical area and every ecological niche within each area. Constant selection-pressure will be exerted, causing adaptive trends, once begun, to be specialized toward a limit [explaining "orthogenesis"].

Release from competition has permitted abnormal variability and multiplicity of forms, not only for species and subspecies but for entire groups [explaining "explosive evolution"]. Originally adaptative structures or functions degenerate in the absence of further selection-pressure in their favour [explaining "degenerate evolution"].

The treatment of speciational processes is superlatively fine. Huxley demonstrates a marvelous command of factual data for all main groups of plants and animals. He avoids the restricted view of a specialist in only one group. His more pointed expressions on speciation may be organized thus:

There are a number of quite different *kinds* of animal and plant species, differing in their mode of origin and in their biological characteristics. We can distinguish four main kinds of species, the successional, the geographical, the ecological, and the genetic [long emphasis is given to the role of polyploidy in the speciation of plants]. Species-formation may be continuous and successional; continuous and divergent; abrupt and convergent; or *reticulate*.

Parallelism may lead to forms which are taxonomically indistinguishable, being evolved independently in several areas. Groups may remain perfectly

distinct though morphologically indistinguishable, but subspecies may differ visibly more than do good species.

Specific systems become mutually inharmonious or even incompatible through the sheer accumulation of difference. Isolation is *per se* a cause of differentiation. The smaller the size of a natural population and the more perfectly it is isolated, the more likely is drift to proceed to its limit [the Sewall Wright effect, much emphasized].

We must use a combination of several criteria in defining species. Undoubted species may cross and yield fully fertile hybrids. In most cases a species can be regarded as a geographically definable group, whose members actually interbreed or are potentially capable of interbreeding in nature, which normally in nature does not interbreed freely or with full fertility with related groups, and is distinguished from them by constant morphological differences.

I have read many simpler species concepts, but none that has appealed to me as a truer rendering of the facts.

While avoiding the idea of Goldschmidt that "microevolution" is something entirely apart from evolution proper ("macroevolution"), Huxley rightly holds that "much of the minor systematic diversity to be observed in nature is irrelevant to the main course of evolution"—a sort of veneer. Sudden creation of entirely new "reaction systems" do not appeal to Huxley as the mode of speciation. Rearranging selected sentences we find his view to be that:

Sudden and unadjusted advance is impossible. Most adaptive specialization therefore cannot help but be gradual. The mutations that are of value for evolution will in most cases be of very small extent, of slight effect. Evolution will in general proceed, not by the selection of single mutations, but by the selection of mutations in relation to a favourable combination of existing small gene-differences. Single-gene differences between species must be enormously numerous. Gone is any notion of species in higher animals arising by a single mutation, or even by a few steps. Evolution consists in the accumulation and integration of very numerous and mostly small genetic changes.

Major evolutionary trends, whether classed as specialization or as progress, are to Huxley real phenomena, distinct from (though comprising) the endless array of intraspecific and interspecific differentiations. He presents—though briefly and scatteringly—well worded statements on fundamental principles of phylogeny. Some of his key thoughts may be brought together:

When a group is considered as a whole, it will be found in the early stages of its history to be radiating in a number of trends. Evolution is essentially divergent. However, in certain long-range evolutionary trends in animals, parallel changes appear to have played a greater part than was formerly supposed [the "horizontal series" of paleontologists are stressed].

Dominant types [groups] are characterized not only by a high degree of complexity but by a capacity for branching out into a multiplicity of forms. In each epoch a minority of stocks gives rise to the majority, in the next phase, while the majority of the rest becomes extinguished or reduced. This radiation seems always to be accompanied by the partial or even total extinction of competing main types.

The further a trend toward specialization has proceeded, the deeper will be the biological groove in which it has thus entrenched itself. Thus specialization, in so far as it is a product of natural selection, automatically protects itself against the likelihood of any change save further change in the same direction. The result is apparent orthogenesis.

Huxley turns away from reading "purpose into evolution, as earlier men projected will and emotion into inorganic phenomena like storm or earthquake." He strikes out for an inductive concept of evolutionary progress and arrives at an interesting philosophy, which, by again selecting and rearranging the author's key pronouncements, may be expressed as follows:

The distinguishing characteristics of dominant groups all fall into one or the other of two types—those making for greater control over the environment, and those making for greater independence of the environment. Thus advance in these respects may provisionally be taken as the criterion of biological progress. Evolutionary progress consists in a raising of the upper level of biological efficiency. Progress is all-round biological improvement; specialization is one-sided biological improvement. Progress is not the same as specialization. Specialization is an improvement in efficiency of adaptation for a particular mode of life: progress is an improvement in efficiency of living in general. Natural selection can account for progress as well as adaptation. There is no more need to postulate an *élan vital* or a guiding purpose to account for evolutionary progress than to account for adaptation, for degeneration or any other form of specialization.

Only along one single line is progress and its future possibility being continued—the line of man. Man is not within the near future destined to break up into separate radiating lines. For the first time in evolution, a new major step in biological progress will produce but a single species. The future of progressive evolution is the future of man. Man, by now become the trustee of evolution, must work and plan if he is to achieve further progress for himself and so for life.

Distribution and Variation of the Hawaiian Tree Snail Achatinella apexfulva Dixon in the Koolau Range, Oahu. By D'ALTÉ A. WELCH. Smithsonian Miscellaneous Collections, 103, 1942: 1–236, pls. 1–12, figs. 1–8. $1.00.

RETREADING the ground made famous by the speciational researches of Gulick and of Pilsbry and Cooke, and covering it much more thoroughly, d'Alté A. Welch has built up for us, in this work as in a similar, previous treatise,[1] a noteworthy picture of local differentiation on an amazingly fine scale. In a single mountain range with maximum dimensions of about 12 by 35 miles, in which the tree snails are largely confined to the spurs from the main mountain ridge, there are recognized in the one species 78 subspecies, many of which are further divided into numbered races ("varieties"). The species and subspecies concepts are those of the vertebrate zoologist: species are set apart on the basis of nonintergradation, and subspecies are recognized for the local races that are distinct enough to warrant naming.

This intense speciation is correlated with the highly localized and apparently rather stabile nature of the populations. Each local form tends to have some peculiar features of color or form (of the shell), and regional complexes show certain common features, particularly in the color of the embryonic whorls. Populations intervening between subspecies often show intermediate or mixed characteristics. Some features exhibit ecologically correlated gradients.

In the maze of noncorrelated individual variations, however, the author had to search long and hard for characters that follow the conventional association with locality and with climatic gradients. By far the most striking peculiarities in shape and color occur within unit populations and are repeated almost endlessly not only in forms of adjacent ranges but also in those that are well

[1] Distribution and Variation of Achatinella mustelina Mighels in the Waianae Mountains, Oahu. Bernice P. Bishop Museum, Bull. 152, 1938: 1–164, pls. 1–13, maps A and 1–16, fig. A. The 4 other species of the genus as recognized by Welch remain to be treated by him.

separated (in the microgeographic pattern). The shells twist dextrally or sinistrally almost with abandon; adjacent stocks may be predominantly of opposite twist. Plain, banded and striped color patterns occur on both globose and elevated shells, all at single localities. The subspecies to a large degree are characterized by the relative proportions of these individual variations, and are therefore ordinarily identifiable only by series.

Welch's main contribution has been to establish the precise geographical pattern of the local kinds, rather than to make an intensive analysis of the geographical and individual variation. In fact the only character subjected to statistical analysis, save for the relative proportions of color types that are given for a few forms, is the height of the shell (which may not be genetic), and for this character only the range and the means are presented. Two other shell dimensions (width of shell and height of spire) are given only for specimens of median height, or for extreme variations in height. A statistical analysis of measurements of shell height and width, of spire height, and of length and width of aperture, and particularly of ratios between these dimensions, might afford a basis for a more objective treatment of these variable snails. Experimental studies—at least transferences of populations—are also much needed. Such tasks would be enormous, but we hope may be undertaken, at least for a small area, when peace returns to Hawaii.

NOTICES OF NEW BOOKS

Common Edible Mushrooms. By CLYDE M. CHRISTENSEN. Minneapolis: University of Minnesota Press, 1943: i–x, 1–124, col. pls. 1–4, diags. 1–2, figs. 1–62.—Designed to serve the individual who has had no previous experience with fungi, this publication, contrary to the title, contains accounts of both edible and poisonous species. The term "mushroom" is used to embrace all fungi, a usage which many people will be inclined to question. Although descriptive accounts of the various species are included, the illustrations are the most valuable aid to identification. Many

of the halftones are very good. Fig. 49, however, probably represents *Coprinus micaceus* instead of *C. atramentarius.* The four color plates are disappointing because the colors shown for many of the species are not true to life. *Collybia velutipes, C. platyphylla, Hypholoma sublateritium* and *Lepiota Morgani* are outstanding in this respect. *Lactarius cilicioides,* listed as edible, has been treated as poisonous by some specialists, and because of its similarity in appearance to *L. resimus* and certain forms of *L. torminosus,* must be regarded as dangerous. On page 48 an unfortunate misstatement is made, *i.e.,* ". . . a mushroom that *exudes droplets of a white or colored liquid* is invariably Lactarius." Actually *Mycena haematopus* possesses a dark red juice, and when its gills are broken, droplets are sometimes exuded. Since this is a very common species, every collector is sure to find it sooner or later.—ALEXANDER H. SMITH.

Biology The Science of Life. By MARY STUART MACDOUGAL AND ROBERT HEGNER. New York: McGraw-Hill Book Co., 1943: i-x, 1–963, figs. 1–555.—The authors have handled well the difficult task of illustrating fundamental biological principles with both plant and animal examples. Ample treatment is also given to the development of an appreciation of plant and animal groups by a study of types. Progressive features are the chapters on applied biology: Biology and Human Welfare; Conservation. Many of the illustrations are new and are good except for the sketches used to illustrate the groups of organisms. Inclusion of the derivation of technical words where they occur in the text is commendable, serving to make scientific terms come to life, and the glossary is exhaustive. The length of the book will preclude its use as a text in any but the longer types of courses.—KARL F. LAGLER.

The Wild Turkey in Virginia: Its Status, Life History and Management. By HENRY S. MOSBY AND CHARLES O. HANDLEY. Richmond, Va.: Game Commission of Game and Inland Fisheries, 1943: i–xx, 1–281, frontisp., figs. 1–68. $1.00.—An excellent monograph in the field of applied ecology.

Meeting the Mammals. By VICTOR H. CAHALANE. New York: Macmillan Co., 1943: i-ix, 1–133, 52 figs., 1 map. $1.75.—In this guidebook there are 66 short, intimate, readable, sometimes anthropomorphic biographies of the mammals that might be encountered in our western national parks. It is written for the interested tourist, who will want a copy in his library. Most of the natural history is good. The interesting illustrations by Walter A Weber add much to the usefulness of the volume.—WILLIAM H. BURT.

The Ring-neck Snakes, Genus *Diadophis*. By FRANK NELSON BLANCHARD. Bull. Chicago Acad. Sci., 7, 1942: 1–144, figs. 1–26, maps 1–4. $1.25.—This posthumous work lives up to the Blanchard tradition of impersonal outlook, careful, cautious presentation of data and meticulous, precise style. Much credit must go to Dr. Gloyd, of the Chicago Academy of Sciences, whose deep and intimate understanding of the author is evident in the excellent editing of the paper.

The lack of an introduction is to be doubly regretted since it is quite certain that one had been prepared which is thought to have stated the author's views on speciation in snakes in general.

As has been shown for *Pituophis*, *Thamnophis* and other snake genera, *Diadophis* differentiated and spread from a southwestern center. The chief similarities evolved in the end forms to the East and to the West are the lack of ventral pigmentation and the reduced number of scale rows. The western derivatives have retained the primitive dentition but have acquired larger bodies while the eastern races have developed more maxillary teeth and shorter bodies.

An unusual feature, or at least an unusual interpretation of evolutionary sequences in herpetology, is found in the author's speculations on the intraspecific relationships of the races of *D. punctatus*. He hypothecated that the Ozarkian upland form is ancestral; that it became reduced in size and number of scales, as it migrated southward into the Mississippi and Gulf lowlands, to form a new race. These features were retained as the lowland race spread and evolved into another lowland race in the southeastern United States. But, when the southeastern reduced form moved northward into the Appalachian upland habitat (similar to the ancestral one) it evolved into another race which was larger and had a greater number of scales, simulating its ancestor of the Ozarks. If this interpretation be correct, certainly the evidence is strong that the changes taking place with the spread of the species were adaptive, as Fitch found in the western garter-snakes, and not orthogenetic.

The author's use of the term hybridization, as contrasted with intergradation, is somewhat confusing. He apparently uses it to indicate interbreeding not only between distinct species but also between any two subspecies, in the same racial group, which do not have the immediate progenitor-descendant relationship. Intergradation is reserved to indicate interbreeding only between direct-line relatives.

Dr. Blanchard had been actively interested in the natural history of the genus for many years as attested to by other publications and the well-chosen, detailed observations under "Habits" and "Habitats" in the present one.—NORMAN HARTWEG.

SHORTER ARTICLES AND DISCUSSION

ON WHEELER'S PAPER CONCERNING EVOLUTION AND THE NEMERTEAN *GORGONORHYNCHUS*

THIS note has been inspired by the detailed, stimulating, extensive paper by Dr. J. F. G. Wheeler, entitled "The Discovery of the Nemertean *Gorgonorhynchus* and its Bearing on Evolutionary Theory."[1] I am not especially interested in the study of worms, and I certainly would not have recognized a *Gorgonorhynchus* before reading Dr. Wheeler's paper. I have, then, no authority to discuss worms. However, I justify this writing on the basis of my being a student of biogeography, evolution and insular biotas.

In 1932, Dr. Wheeler found a nemertean in Bermuda which is most unusual in that it has a proboscis that is many-branched rather than being of the normal simple type found in all previously known nemerteans. He later described it as a new species of *Cerebratulus*. However, a presumably congeneric species, made the type of the new genus *Gorgonorhynchus* (unknown at the time to Dr. Wheeler), had been found in 1930 in Australia and is now known from several Australian localities. Dr. Wheeler notes that the reefs of Bermuda have been scoured by experienced collectors for years and large collections of worms assembled, but that no one had found *Gorgonorhynchus* in Bermuda before he discovered it. He comes to the highly probable but not certain conclusion that the worm has habits which would have led to its discovery had it been there during the surveys made by Verrill, Coe and others (but might it not have been in Bermuda then, at a low stage in a major cycle of abundance?). He says (p. 481) "It should be observed that *this is the only case that has ever been presented of the discovery of a new type in a small and uniquely isolated locality that had been examined many times previously not only by trained observers but by specialists in the group of animals to which the type belongs.*" The discovery of two species of such a unique genus in two widely separated localities at such recent dates has led Wheeler to summarize a large body of data, and he says, "I have ventured to put forward my view because it carries my conception of the gene to a natural conclusion and because it appears to offer an explanation of what to me is an incredible coincidence."

The "incredible coincidence" which has caused Wheeler to

[1] AMERICAN NATURALIST, 76: 766, 470–493, September–October, 1942.

summarize his views regarding evolution is that these remarkable worms have arisen in Bermuda and Australia spontaneously, "*de novo*," at the same time. Dismissing the possibility of a recent introduction, he believes that the worm suddenly appeared in Bermuda because it explosively developed from some other species in Bermuda. He says (p. 480) "It is, of course, conceivable that *Gorgonorhynchus* could have been introduced recently into Bermuda either in the natural course of its own methods of distribution or by artificial and presumably accidental transport, and, that, following introduction, it rapidly and successfully colonized the beaches. What data we have count against a natural introduction, for, though it may be asserted with some truth that the nemertean fauna of the world is relatively little known, such a conspicuous type would almost certainly have been observed." The possibility of its accidental importation by man is, says Wheeler, ". . . not worth consideration." And, further, he says "By eliminating the possibility of recent introduction we face a clear-cut alternative: either *Gorgonorhynchus* was present all the time but remained undiscovered by Verrill, Coe and others, or it has arisen somehow *de novo*, sometime between 1903 and 1932."

After studying the distribution and dispersal of plants and animals for some years, I can not see that the possibility of the recent introduction of *Gorgonorhynchus* in Bermuda has been eliminated. The ways and means of occasional transport of organisms about the world are diverse—and how little we actually know about them! It is common knowledge that various kinds of plants and animals are continually becoming established in strange localities far from their homes. Here in Hawaii, where a keen, active body of naturalists has been working for many years, many hundreds of foreign species have become established and have suddenly appeared in numbers. Every year new ones make their appearance. By what means many of these species got here we do not know, but the fact remains that they did get here and have established themselves, and that some are now common and widespread. Certain of these new-comers have proven to be species new to science, and have been described from Hawaiian specimens, but their places of origin have not yet been discovered. Some of them are utterly different from anything seen in the islands before. Some of them represent orders new to the islands' biota. But that is no wonder, for the world is yet incompletely explored, and the number of kinds of organisms is enormous (there are more than 250,000 described species of

beetles alone), yet that number represents only a part of those that will be described.

About 1900, an immigrant insect new to Hawaii made its appearance, and a short time later it threatened to wipe out the sugar-cane industry throughout the islands. The species was found to be new, and it was so distinct that a new genus had to be erected for it. Its native home was not known. At a later date this insect (now known as the sugar-cane leaf-hopper, *Perkinsiella saccharicida* Kirkaldy) was found to be a native of Australia. However, the environmental pressure of its home country is such that the species is not common and is not considered a pest there. Other species of the same genus have since been described from a number of localities. Parasites and predators have been imported to Hawaii and these have exercised such a successful control upon the insect that it is no longer a serious pest in the islands. The annals of entomology record this history as one of the classic examples of biological control. *Gorgonorhynchus* appears to be one of the common nemerteans of Bermuda. Is it not possible that its abundance has the same basis as that of *Perkinsiella?*

The distribution of *Teredo fulleri* Clapp, 1924, described from the West Indies, is interesting and analogous. Recently Dr. C. H. Edmondson has found that the species had become established in several localities in the Hawaiian Islands, and in 1941 he determined that it had also become established at Apia, the port of Western Samoa. In so far as is now known, this mollusc appears to be found only in these widely separated localities. Another interesting observation is that it appears to be rare in the West Indies, whereas it was found to be excessively abundant in Samoa. It appears obvious to us that the only plausible explanation of this erratic distribution is that the species has been artificially distributed through the unintentional aid of man. There are other examples of marine organisms that occur in Hawaii but are elsewhere known only from distant localities.

Gorgonorhynchus may well have reached Bermuda on ship bottoms. Chilton[2] assembled data regarding the dispersal of marine Crustacea by ships. A specimen of the North American horseshoe crab (*Limulus*) was found at Copenhagen, and an example of a Malaysian species was caught at Auckland, New Zealand. Presumably both individuals had been carried to these distant localities by ships. Any one who has seen the diversity and quantities of marine organisms on the bottoms of dry-docked

[2] *Trans. New Zealand Institute*, 43: 131–133, 1911.

ships, especially those heavy with "weed," could hardly doubt that such vehicles must act as effective agents of dispersal.

It appears most probable that *Gorgonorhynchus* has been accidentally imported to Bermuda in recent years. Need it have been imported all the way from Australia? Perhaps the genus has a wider distribution than is now known, and, if so, there may be localities nearer to Bermuda where it will be found. Attention should also be given to the possibility that both the Australian and Bermuda species have been introduced from some region where they are, perhaps, rare and where they have not yet been found. The nemerteans have received little critical study in the tropical Pacific as a whole. The routes of ships, large and small, are often quite distinct from the regular steamer lanes marked on the maps. Yachts, warships and other craft put into island ports from all corners of the world, and some of these might bring in odd creatures from strange lands. Only further collecting will elucidate such problems of distribution, and I believe that it is safe to assume that the species of *Gorgonorhynchus* now known only from Bermuda will be found elsewhere. The erection of evolutionary theory upon such incomplete information is not justified.

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A FACTORIAL EXPERIMENT ON THE MINERAL REQUIREMENTS OF A *DROSOPHILA* CULTURE

INTRODUCTION

Drosophila melanogaster has been bred on a diet containing K_2HPO_4 and $MgSO_4$ as the sole salts (Loeb, 1915), NaCl and $CaCl_2$ being present only as impurities. Both the potassium and the phosphate were essential and no flies could be raised if sodium was substituted for potassium; a fly occasionally developed on potassium phosphate alone. In reporting these results Wigglesworth (1939) remarks that "it is unknown what the larvae contrive to pick up from the impurities, for no analysis of the larva ash was made." It is obvious that in Loeb's experiments nitrogen must have been present in organic form, probably in the yeast on which *Drosophila* usually feeds. Making use of these and similar results Pearl (1928) and his collaborators developed an elaborate synthetic medium for a yeast culture of *Drosophila* containing in addition to agar (2 per cent.), cane sugar (8 per cent.), and tartaric acid (0.5 per cent.), five salts in the following concentrations:

Ammonium sulfate $(NH_4)_2(SO_4)$	0.2	per cent.
Epsom salt $MgSO_4$, $7H_2O$	0.05	" "
Calcium chloride $CaCl_2$	0.025	" "
Primary potassium phosphate KH_2PO_4	0.1	" "
Rochelle salt $KNaC_4H_4O_6$, $4H_2O$	0.8	" "

As Pearl's medium is still widely used, it is as well to investigate whether the five salts mentioned are necessary in *Drosophila* cultures and whether some may not even be harmful. In addition, it is of interest to determine whether they are given at the optimum concentration. Factorial experiments, so successful during the past few years in agriculture (Yates, 1937), may be expected to give an answer to these questions in a much shorter time than was possible at the time of Pearl's experiments. The determination of the mineral requirements for the usual two species system (yeast-*Drosophila*) may be regarded as a first step towards determining the minimum requirements of *Drosophila* under sterile conditions.

Material and Method

A Swedish wild-type stock was used in all experiments. Two males and three females, all three to four days old, were kept for a week on the media and then released. The temperature was 27° C, the relative humidity 70 per cent. All the offspring were counted.

In the first factorial series 1,570 flies were bred in 192 vials, each containing 10 cc of 2 per cent. agar solution with 8 per cent. sucrose, 5 per cent. tartaric acid and some cellucotton (cellulose) to give the mixture a higher consistency. Following Pearl's prescription .008 gm Rochelle salts (R), .002 gm ammonium sulfate (A), 0.0025 gm calcium chloride (C) and 0.005 gm Epsom salts (E) were added to the solution singly and in all possible combinations. Potassium phosphate was used at three levels, 0.00 gm, 0.005 gm (P_1) and 0.015 (P_2), Pearl's value being between these last two (0.01 gm).

Sixteen combinations were tested in the absence of phosphate and at the two phosphate concentrations mentioned above. Their constitution was as follows: (1), R, A, RA, C, RC, AC, RAC, E, ER, EA, ERA, EC, ERC, EAC, ERAC.

Of these 48 experiments four replicates were made, giving a total of 192. After cooling the vials were sprayed with a very dilute emulsion of yeast in water.

RESULTS

Of the results obtained only a few need rigorous treatment by analysis of variance, an example of which will be given later. The most important ones can be summarized as follows:

(1) Influence of KH_2PO_4:

In 64 vials containing no potassium phosphate	1	fly hatched
" " " " 0.005 gm " "	631	flies "
" " " " 0.015 gm " "	938	flies "

From these figures it can easily be seen that potassium phosphate is necessary for the development of *Drosophila* and that an increase from 0.05 per cent. to 0.15 per cent. increases the yield. The one fly hatched in the absence of potassium phosphate developed while potassium was available in the form of Rochelle salt, but phosphate was lacking.

(2) Influence of $(NH_4)_2(SO_4)$:

In 96 vials containing no ammonium sulfate	43	flies hatched
" " " " 0.02 gm " "	1,527	" "

Thus it is clear that ammonium sulfate greatly favors the development of *Drosophila*.

(3) Influence of $MgSO_4$, $7H_2O$:

In 96 vials containing no Epsom salt	492	flies hatched
" " " " 0.005 gm " "	1,088	" "

The addition of $MgSO_4$ raised the yield in each of the eight cases, where potassium phosphate and ammonium sulfate were present. At the higher phosphate concentration the numbers of flies were for P_2A: 19, 11, 35, 25, and for P_2AE: 54, 67, 57, 39. They show a highly significant difference.

Epsom salt, although not so essential for the breeding of *Drosophila* as potassium phosphate or ammonium sulphate, nevertheless approximately doubles the yield of flies.

(4) Influence of $CaCl_2$:

In 96 vials containing no calcium chloride	805	flies hatched
" " " " 0.0025 gm " "	765	" "

Calcium chloride seems therefore to have little effect on the yield of flies.

(5) Influence of $KNaC_4H_4O_6$, $4H_2O$:

In 96 vials containing no Rochelle salt	996	flies hatched
" " " " 0.08 gm " "	574	" "

Rochelle salt thus decreases the yield.

Table I summarizes the results of all the experiments with K_2HPO_4 and $(NH_4)_2SO_4$, and shows the interaction of C, E and C E with R at both phosphate levels.

TABLE I

		P_1	P_1R	P_2	P_2R
		101	17	90	43
C		68	41	33	76
	E	125	66	217	128
C	E	140	50	213	117

From this factorial experiment it would appear that in Pearl's medium calcium chloride is unnecessary, Rochelle salt detrimental and the other three salts necessary. In addition an increase of the concentration of potassium phosphate increases the yield.

Having eliminated two of the constituents, the next step is to find out whether an increase in concentration of the three remaining salts can increase the yield. For this purpose a three-level experiment was made using potassium phosphate, at 0.2, 0.3 and 0.4 per cent., ammonium sulfate at 0.3, 0.4 and 0.5 per cent. and Epsom salt at 0.08, 0.16 and 0.24 per cent. The total yield in the media was less than those obtained at the highest phosphate level in the first experiment, and there was nowhere a significant increase in yield. It would therefore appear that a further increase of the three salts beyond the maximum used in the first factorial experiment is not profitable. By offering P and K in proportions different from those contained in KH_2PO_4 it might be possible still further to increase the yield; but such an increase would probably not be worth the increased complications of method.

Summary

In this paper a synthetic medium is described for breeding *Drosophila* and yeast, which is simpler in composition than Pearl's, and gives higher yields.

Of the five mineral salts used in Pearl's medium, calcium chloride has been found to be unnecessary, and Rochelle salt detrimental. The yield of flies can be increased by increasing the concentration of KH_2PO_4 from 0.1 per cent. to 0.15 per cent. Pearl's concentrations for ammonium sulfate, 0.2 per cent., and Epsom salt, 0.05 per cent., are very near the optimum.

The composition of the medium is as follows:

H_2O	891 gm
Agar	20 "
Tartaric acid	5 "
Sucrose	80 "
KH_2PO_4	1.5 "
$(NH_4)_2SO_4$	2 "
$MgSO_4, 7H_2O$	0.5 "

H. Kalmus

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STUDIES ON INDUCTION OF MUTATIONS BY CHEMICALS. I. EXPERIMENTS WITH HEAVY WATER (DEUTERIUM OXIDE)

VARIOUS chemicals have been tried with a view to inducing mutations; and in some cases (iodine, copper sulfate), apparently significant increases in mutation rate have been reported. These results have been questioned, however, both because the increase in mutation rate was rather small, and because it has not been proved that the chemical substance used actually penetrated into the nucleus (review in Dobzhansky, 1941, p. 46).

The problem of penetration of chemicals into a living nucleus is one of primary importance in studies of this kind. If the chemical is introduced (by feeding or injection) into the body of a higher organism, it has to penetrate many cellular membranes before it can reach the nuclei of the germ cells to produce germinal mutations. If the Drosophila egg is exposed to chemicals, the cellular membranes of particular cells may not be formed yet if the egg is very young, but still the chemical has to penetrate the vitelline membrane of the egg. In both cases, because of the selective permeability of the living membranes, the probability of penetration of introduced molecules is very low, especially where the vitelline membrane is present.

In the present experiments, heavy water (deuterium oxide) was chosen as the chemical agent, partly because its introduction into a living nucleus involves no more difficulty than the introduction of water, the permeability of cellular membranes and the ingestion in food being similar for water and for heavy water (Krogh, 1938). Consequently, if any organism is raised on food containing a high concentration of heavy water, that organism, including nuclei and genes, will be partially built out of heavy water. This has been shown for a wide variety of organisms,

including yeast (Salzer and Bonhoffer, 1936), algae (Bonhoffer, 1938; Reitz and Bonhoffer, 1935), fishes (Hevesy, 1935) and mice (Rittenberg and Schoenheimer, 1937; Stekol and Hamill, 1937; Smith, Trace and Barbour, 1936). The most efficient way of introducing deuterium into Drosophila is to raise the larvae and flies on food containing deuterium. Another way is to inject heavy water into the body cavity of the larva, in which case it may be expected that the deuterium will penetrate the gonads and affect the germ cells.

As a rule, if water containing deuterium reaches an organic compound, hydrogens that are connected with N and O exchange with the deuterium almost instantly (Reitz, 1938; Bonhoffer, 1938), in a ratio which tends to correspond to the deuterium/hydrogen ratio in the surrounding water (Wirtz, 1937; Ogawa, 1936). This exchange is easily reversible, and if pure water subsequently reaches this compound all the deuterium is replaced again by hydrogen. Hydrogen connected with carbon, on the other hand, is not so readily interchangeable with deuterium (Reitz, 1938; Bonhoffer, 1938); the exchange may take days, and at all times the concentration of deuterium reached in the organic compound is lower than in the water surrounding the compound. In the latter case, moreover, the exchange is not so easily reversible, and deuterium connected with carbon remains in the organism for many days or even weeks (Hevesy, 1935; Smith, Trace and Barbour, 1936) after feeding with the food containing deuterium has been discontinued.

The above-described substitutions have been shown to occur not only in the living organism but also in a variety of organic compounds, including amino acids and proteins (Salzer and Bonhoffer, 1936; Stekol and Hamill, 1937).

In the present study, one generation of *Drosophila melanogaster* was raised on or injected with a solution of heavy water in ordinary water; and deuterium was thus given an opportunity to serve as a substratum for building new genes, as well as to replace hydrogen in the already existing genes. Offspring of the individuals raised on deuterium, and thus presumably containing genes rich in heavy hydrogen, were raised on ordinary food; and consequently the genes of the second-generation flies were allowed to revert to hydrogen structure. It was hoped that, since the properties of deuterium are somewhat different from those of hydrogen, the highly complicated molecule of the

gene might be affected by the change from hydrogen to deuterium and back to hydrogen. It was also hoped that this double exchange of hydrogen-deuterium-hydrogen might not be strictly reversible; in other words, that somewhere within this process a mutation in a gene might be induced.

EXPERIMENTS

In the first series of experiments, wild-type flies of Swedish-B stock were raised on standard banana-agar food containing 40, 55.2 and 60 per cent. of heavy water. Forty per cent. is used here to mean 40 weight units of pure deuterium oxide per 100 units of liquid present in the food. Heavy water was furnished by the Stuart Oxygen Company. Water content of the bananas used (about 74 per cent.) was experimentally determined, and 95 per cent. heavy water was added in the quantity adequate to obtain the desired concentration. In the second series, Oregon-R flies were raised on banana food containing 40 per cent. and 60 per cent. of heavy water. The doses 40 and 55.2 per cent. were sub-sterilizing. In the third series, 29 old larvae (just before pupation) of Oregon-R stock were injected with small quantities of 40 per cent. heavy water, and 24 larvae with small quantities of 95 per cent. heavy water. In the Oregon-R series of experiments, the sperm of the emerging males was tested for sex-linked lethals by means of the standard C1B method on regular food containing no heavy water. The numerical data are given in Table I.

TABLE I

RESULTS OF TESTS FOR X-CHROMOSOME LETHALS OF MALES RAISED ON FOOD CONTAINING DEUTERIUM OR INJECTED WITH DEUTERIUM IN LATE LARVAL STAGE

Treatment	Concentration per cent.	No. of flies hatched or larvae injected	No. of fertile males	No. of sperms tested	No. of lethals
Deuterium in food	40	28	13	1496	1
	40	7	4	344	–
Deuterium injected	40	29	7	187	–
	95	24	2	133	–

RESULTS AND DISCUSSION

Not all the eggs of flies kept on 40 and 55.2 per cent. deuterium food hatched, and only a few larvae pupated and emerged as imagoes. The larvae from cultures kept on 60 per cent. deuterium did not pupate at all. Fifty-eight per cent. of larvae injected with small quantities of 40 per cent. deuterium survived

and developed normally, and so did 12 per cent. of the larvae injected with small quantities of 95 per cent. deuterium.

Various physiological and developmental effects of heavy water on organisms have been reported. In Drosophila, Schmidt-Nielsen and Schmidt-Nielsen (1936) found that reproduction stops at a concentration of 51.5 per cent.; the simpler organisms, for instance yeast cells, can reproduce at 75 per cent. concentration.

The effects of heavy water on development are, at least in part, caused by the fact that heavy water changes (Bonhoffer, 1938), mostly depresses, the velocity of enzymatic reactions. The sterility observed in the present experiments is probably also due to the upsetting of delicately timed and balanced patterns of enzymatic reactions.

The numbers of sex-linked lethals found in C1B analysis were not higher than the numbers found in untreated Oregon-R flies (Demerec, 1937); this suggests that deuterium did not cause any increase in mutation rate.

It has been stated before that organic compounds on deuterium substratum must also contain some deuterium atoms in place of hydrogen. From the analogy with amino acids and proteins it may be estimated that in the present experiments the genes contained up to 30 per cent. of C-connected deuterium and up to 40 per cent. of N- and O-connected deuterium in place of hydrogen; yet this did not permanently affect the structure of the gene.

There are at least two possible explanations of these results. One is that the substitution of deuterium for hydrogen did not change either the structure or the activity of the gene. The other possibility is that the gene structure was affected but was able to return to its original form as soon as the deuterium was again replaced by hydrogen.

These results may be similar to the results on virus reported by Miller and Stanley (1941). These investigators found that even if 83 per cent. of amino groups in the virus molecule are acetylated, this molecule, although so considerably changed, nevertheless reproduces in completely normal form.

Summary

Heavy water (deuterium oxide) was introduced into Drosophila eggs and larvae by feeding and by injections. Owing to the high permeability of the cell membranes, similar to the permeability for pure water, it is very likely that deuterium was utilized in building the gene molecules. Concentrations of 60

per cent. in food prevented the hatching of eggs. At lower concentrations, given in food and as injections, a few flies were obtained. These were tested by means of the standard C1B method on regular food. The test did not show any increase in mutation rate. It is concluded that the deuterium in the gene molecule did not change its structure or else that this structure was temporarily changed but reverted to the original form when deuterium was eliminated from the organism.

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